Patterns and drivers of fungal disease communities on Arabica coffee along a management gradient

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Abstract

Plants, including those managed by humans, are often attacked by multiple diseases. Yet, most studies focus on single diseases, even if the disease dynamics of multiple species is more interesting from a farmers’ perspective. Moreover, most studies are from single management systems, although it is valuable to understand how diseases are distributed across broad management gradients, especially in cases where less intensive management also provides biodiversity values in the landscape. To understand the spatial dynamics and drivers of diseases across such a broad management gradient, we assessed four major fungal diseases on Arabica coffee (Coffea arabica) at 60 sites in southwestern Ethiopia along a gradient from only little managed wild coffee in the forest understory to intensively managed coffee plantations. We found that environmental and management factors related to disease incidence and severity differed strongly among the four fungal diseases. Coffee leaf rust (Hemileia vastatrix) and Armillaria root rot (Armillaria mellea) were more severe in intensively managed sites, whereas coffee berry disease (Colletotrichum kahawae) and wilt disease (Gibberella xylarioides) were more severe in less managed sites. Among sites, incidence and severity of the four fungal diseases poorly correlated with each other. Within sites, however, shrubs that were severely attacked by coffee leaf rust also had high levels of berry disease symptoms. A better understanding of disease dynamics is important for providing management recommendations that benefit smallholder farmers, but also to evaluate possibilities for maintaining biodiversity values in the landscape related to shade cover complexity and wild coffee genetic variation.

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Keywords: Coffee; Coffee fungal diseases; Co-occurrence; Disease community; Management gradient; Southwestern Ethiopia

Introduction

While plants are frequently attacked by multiple diseases, the majority of studies on the spatial and temporal dynamics and drivers of diseases in natural and agricultural systems have focused on the disease dynamics of single species
(Avelino et al., 2006; Tack, Thrall, Barrett, Burdon & Laine, 2012). Hence, we lack insights into the distribution and dynamics of disease communities; whether diseases attacking the same host plant respond to similar abiotic and biotic drivers or not and if they are co-distributed. Moreover, the majority of studies on disease systems have focused on either natural or agricultural diseases, and the link between disease dynamics in natural and agricultural systems is less investigated. A promising location to study this link is the plant's area of origin, where the diseases occur natively on wild plants as well as on the managed crop. As a way forward, we need to study multiple diseases occurring on the same host plant across a management gradient spanning from natural to agricultural systems.

Given the dominance of studies focusing on single plant diseases (Bolton, James & David, 2008; Marçais & Desprez-Loustau, 2014), our understanding of disease community dynamics is pieced together from disparate studies on single diseases on the same or different host plants in different areas across the world. Such single species studies do not give insights into disease co-occurrence patterns, the degree to which diseases respond to the same drivers, and the additive or synergistic effects of single versus multiple attacks on plant fitness. As one example of a study on multiple diseases in a natural community, Desprez-Loustau et al. (2018) studied the distribution of three cryptic powdery mildew species on oak, and found that the species strongly differed in their distribution, drivers and co-occurrence patterns across spatial scales ranging from a single leaf to the continent.

Furthermore, studies of plant disease have generally focused on the dynamics of diseases either in their natural environments (Ekholm, Roslin, Pulikkien & Tack, 2017; Jousimo et al., 2014) or in human-altered agroecosystems (Avelino et al., 2007; Bedimo et al., 2008). A few studies focus on variation in disease dynamics along gradients of landscape complexity (Kebede, Baudron, Bianchi & Tittonell, 2018; Soto-Pinto, Perfecto & Caballero-Nieto, 2002), but studies of diseases on crops where the plant is both cultivated and growing wild in the same landscape are lacking. Yet disease dynamics are likely to vary along such gradients, for example due to the fact that host and parasites can freely co-evolve in natural systems, whereas evolutionary changes in agricultural systems are driven by human-imposed artificial selection (Chen, Gols & Benrey, 2015).

Arabica coffee (Coffee arabica L.) is grown in a large diversity of management systems across the tropical world (Moguel & Toledo, 1999; Perfecto, Rice, Greenberg & Van der Voort, 1996) and is, as most crops, attacked by a large diversity of diseases and insect pests (Avelino, Allinne, Cerda, Willecocquet & Savary, 2018). It mainly originates from southwestern Ethiopia, where more or less wild populations with high genetic diversity are still present in larger forest tracts (Anthony et al., 2002; Tesfaye, Govers, Bekele & Borsch, 2014). In southwest Ethiopia, the density and diversity of shade trees vary strongly across the landscapes: in the most intensively managed sites, coffee is grown under a sparse canopy layer made up of one or few tree species, while at the natural end of the gradient coffee berries are harvested from naturally established shrubs under a more or less intact canopy of the montane forest (Gole, Borsch, Denich & Teketay, 2008). Of major concern in Ethiopian coffee systems are several fungal diseases (Hindorf & Omondi, 2011) which often can be found together in the same sites or on the same coffee plant.

Here, we studied the distribution and co-occurrence patterns of four major fungal diseases (coffee leaf rust, coffee berry disease, coffee wilt disease and Armillaria root rot) at 60 Arabica coffee sites in southwestern Ethiopia along a broad management gradient. More specifically, we addressed the following questions:

(i) To what extent do fungal diseases vary in their incidence and severity within and among sites?
(ii) What are the impacts of the abiotic and biotic environment and management intensity on the incidence and severity of the major fungal diseases?
(iii) What is the pattern of co-occurrence of the fungal diseases along the management gradient?

Materials and methods

Study system

This study was conducted in Gomma and Gera districts of Jimma Zone, southwestern Ethiopia (7°37’ - 7°56’ N and 36°13’ - 36°39’ E, Fig. 1A and B). The altitude of the study area ranges from 1500 to 2100 m a.s.l. The area receives an annual rainfall in the range of 1480 to 2150 mm, with the main rainy season between June and September, and has mean daily minimum and maximum temperatures of 12°C and 28°C, respectively. The study area has a mosaic landscape with tree-covered areas such as forests and shade coffee plantations but also open areas for annual agriculture (Lemessa, Hylander & Hämäck, 2013). The climax vegetation in this region is moist Afrotomante forest with mostly evergreen trees such as Syzygium guineense, Schefflera abyssinica, Prunus africana, Pouteria adolfi-friedericii, Ficus sur and Olea welwitschii (Friis, Sebsebe & Breugel, 2010). Coffee is the main source of cash income for the population in the study landscape (Ango, Börjeson, Senbeta & Hylander, 2014; Dorresteijn et al., 2017) and is grown across the whole landscape under various management intensities. We note that some authors use a terminology in which the coffee growing systems of southwestern Ethiopia are divided into several categories depending on management intensity, i.e. forest coffee, semi-forest coffee, semi-plantation coffee and plantation coffee (Aerts et al., 2011; Hundera et al., 2013). However, our plots are selected from a landscape with a clear continuous gradient in attributes.
such as coffee structure and tree layer composition, and we therefore chose to regard management intensity as a continuous gradient. Coffee generally originates from the natural gene pool and farmer’s landraces or, in a few cases, especially in plantations of private companies, cultivars that are resistant to coffee berry disease. At smallholder level, coffee production in the area is generally organic, while fertilization and use of herbicides is a common practice in the plantations. The main fungal diseases on coffee are: coffee leaf rust (Fig. 2A) caused by *Hemileia vastatrix* that leads to defoliation, the coffee berry disease (Fig. 2B) caused by *Colletotrichum kahawae* that mummifies immature coffee berries, coffee wilt disease (Fig. 2C) caused by *Gibberella xylarioides* and root rot (Fig. 2D) caused by *Armillaria mellea* that kill infected coffee shrubs (see Appendix A for details of the diseases). To our knowledge neither fungicides

**Fig. 1.** Study area and plot design. Panel (A) shows a map of Ethiopia, with the study area in southwestern Ethiopia indicated by a red rectangle. Panel (B) shows an aerial view of the study landscape, where the black dots represent the sixty sites established within the landscape. The landscape is characterized by tree-covered forest areas (dark green) and open areas for annual agriculture (light green). Panel (C) shows the layout of the individual plots. Each plot is 50 × 50 m, with the sixteen focal coffee trees selected at the intersection of 10 m grid-lines within the core 30 × 30 m of the plot (the area marked in grey). Each of the focal coffee shrubs was labelled with a metal tag and forest spray. Shade canopy pictures were taken from five locations, as indicated by the blue dots.
nor insecticides are applied to control diseases or pests in any of the coffee systems in southwestern Ethiopia.

**Study design**

Based on Google Earth pictures and short field visits, we selected 60 sites varying in tree cover complexity (e.g. canopy cover, vertical layers and species richness) and coffee management intensity across the focal landscape (Fig. 1A and B), while aiming to avoid spatial autocorrelation in these variables. In each site we established a plot of $50 \times 50$ m and marked 16 coffee shrubs on intersections of the $10 \times 10$ m quadrants in the central $30 \times 30$ m area (Fig. 1C).

**Assessment of fungal diseases of coffee**

We assessed coffee leaf rust from 3 March to 5 May 2017 taking care to visit different parts of the landscape each day (to avoid biases due to date). Three bearing branches per shrub (from the base, middle and upper part) were selected and assessed for presence/absence of rust pustules/lesions ($\geq 20$ leaves per branch). Newly unfolding leaves on the two nodes at the tip of the shoots were not considered for leaf rust assessment as they are less susceptible (Chala, Chemeda, Girma & Holger, 2010). If no leaves on the selected branches had coffee leaf rust infection, we searched an additional c. 2 min for the presence of infection on the remaining part of the coffee shrub. Coffee berry disease, coffee wilt disease and *Armillaria* root rot were assessed from 19 July to 26 August 2017. Number of bearing branches with coffee berry disease symptom and proportion of berries infected with coffee berry disease were recorded for each of the 16 coffee shrubs per site. The number of coffee shrubs with coffee wilt disease and *Armillaria* root rot symptoms were counted within the $50 \times 50$ m plot. The rust is more severe during the dry season compared to the wet season, motivating the different surveying periods (See also Appendix A). We here define incidence as the proportion of infected out of the total number of coffee shrubs per site (for coffee wilt disease and *Armillaria* root rot) and severity as proportion

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**Fig. 2.** Major fungal diseases of coffee assessed during the study. (A) coffee leaf rust (caused by *Hemileia vastatrix*) spores on the underside of the leaf, (B) mummified coffee beans as a result of coffee berry disease (caused by *Colletotrichum kahawae*), (C) blue-black discoloration of the stem as a result of coffee wilt disease (caused by *Gibberella xylarioides*), and (D) stem cracking and rhizomorph growth in the cracked stem due to infection by *Armillaria* root rot (caused by *Armillaria mellea*).
of leaves/berries infected out of the total number of leaves/berries assessed (for coffee leaf rust/coffee berry disease).

Environmental variables

To assess canopy cover, we took five pictures of the shade tree canopy above coffee height (by elevating the camera with a stick) in the central 30 × 30 m plot from the central and corner quadrants (see Fig. 1C). The pictures were subsequently analyzed using ImageJ software, version 1.50i (Schneider, Rasband & Eliceiri, 2012). Slope of the plot was measured with a clinometer (Suunto Clinometer PMS/360). Density of coffee and non-coffee shrubs was counted in the 30 × 30 m plot. Shade trees with diameter at breast height (DBH) >20 cm were identified and counted in the 50 × 50 m plot. Tree cover in an area of 1 km buffer surrounding each of the 60 sites was measured using ArcMAP (Version 10.6.1) from ArcGIS Desktop from a manually interpreted map of forest polygons. We developed an index based on the typical growth pattern of coffee under different types of management to describe the gradient in management intensity across the sites (see Appendix B). This site level index ranges from 1 (only little managed coffee, often in the natural forest) to 3 (heavily pruned coffee, often in plantations), and will henceforth be referred to as ‘coffee structure index’. We also developed an index involving the main coffee management activities (pruning, nutrition and weeding) to get an impression of how coffee management relates to the different diseases (see Appendix B).

Statistical analyses

To understand the variation in disease dynamics among sites we fitted generalized linear (mixed) models with several predictor variables. For proportion data (coffee leaf rust, branches and berries infected with coffee berry disease, all assessed at the level of individual coffee shrubs), a generalized linear mixed model (GLMM) with binomial distribution was fitted using the lme4 package (Bates, Mächler, Bolker & Walker, 2014). Nine predictor variables (see below) were used as fixed factors. To account for correlation among individual trees within a site, we included the random factor ‘site’. The proportion of coffee shrubs with coffee wilt disease and Armillaria root rot (both assessed at site level) were modelled using a generalized linear model (GLM) with binomial distribution. Partitioning of variance in disease frequencies within and among sites was performed for the fungal diseases surveyed at coffee shrub level using the lme4 package (GLMM). We adopt the approach of McMahon and Diez (2007) to assume that the level 1 random effect (within-site variation) is logistically distributed with mean zero and variance \( \pi^2/3 \). The proportions of within-site and among site variation was calculated as \( \tau_\beta/ (\pi^2/3 + \tau_\beta) \) and \( \tau_\beta/(\pi^2/3 + \tau_\beta) \) respectively, where \( \tau_\beta \) is the level 2 random effect variance retrieved from the fitted models. For all the statistical analyses, we used the statistical software R version 3.5.1 (R Core Team, 2018).

To account for variation along the gradient (e.g. resource concentration, light intensity, microclimate, natural complexity among sites), eight environmental and stand structure variables measured at the site level (altitude, slope, coffee density, proportion of non-coffee shrubs to coffee, canopy cover, shade trees >20 cm DBH, surrounding tree cover, coffee structure index and management index) were proposed to be included in the models. However, prior to the final statistical analysis, we assessed the correlation among the predictor variables and decided to omit management index due to the strong correlation with coffee structure index (see Appendix C: Table C1). We scaled all predictor variables to zero mean and unit variance. Additionally, for coffee leaf rust and berry disease, the sampling date was included as a covariate to account for temporal variation in disease incidence and severity. The models were simplified by repeatedly dropping the predictor variable explaining the least variation in the response variable, using a cut-off \( p \)-value of 0.05 (Crawley, 2012). To validate that the absence of an effect of an explanatory variable was not due to co-variation with other explanatory variables, we also ran separate regression models for each of the dropped variables.

To analyze the relationship between the different fungal diseases, we first ran Pearson correlation tests to see if the severity of the different diseases co-varied among sites. As a second step, and because environmental variables may obscure the relationship between the different diseases, we also checked correlations of the residuals extracted from the full models explained in the previous paragraph. Finally, for diseases assessed at the individual coffee shrub level (leaf rust and coffee berry disease), we fitted a generalized linear mixed effects model (GLMM) with one of the diseases as response variable and the other as a covariate, and site as a random effect, to test for the within site co-variation between the two species.

Results

Variation in the environmental factors and disease levels within and among sites

Environmental and stand structure variables varied strongly among the sixty sites (Table 1). For example, shade canopy cover ranged from 13 to 83% and the number of larger shade trees ranged from 5 to 43 tree individuals (Table 1). Coffee density was generally high, and it was the dominant shrub along the entire gradient (Table 1).

The fungal diseases differed strongly in their site-level prevalence: coffee leaf rust and coffee wilt disease occurred in all or nearly all sites (60 and 57 out of the sixty sites, respectively), coffee berry disease was found in the majority
of sites (46), and Armillaria root rot was present in half of the sites. The severity of coffee leaf rust was highly variable among sites (ranging from 0.1 to 35% of infected leaves), but even more variable among shrubs within sites (Table 2). In contrast, infection of berries by coffee berry disease was more variable among sites than among shrubs within sites (Table 2). While coffee wilt disease and Armillaria root rot were both present in a large fraction of our sites, their incidence within sites was relatively low, with a maximum of 5% of infected coffee shrubs per site (Table 2).

### The relationship between environment, management intensity and severity of fungal diseases

Coffee leaf rust severity decreased with altitude and canopy cover (Table 3, Fig. 3A and B), with the effect of canopy cover only significant in the separate regression model (Table 3). Moreover, coffee leaf rust severity decreased during the survey period, but increased with the surrounding forest area within a 1-km buffer (Table 3). In contrast to the coffee leaf rust, the proportion of branches infected with coffee berry disease, as well as the proportion of infected berries, increased with altitude (Table 3, Fig. 3D and C1). Coffee berry disease was more pronounced on trees with a lower value of coffee structure index, which is characteristic for sites with less intensive management (Table 3, Fig. 3F and C1).

Coffee wilt disease was affected by several environmental variables (Table 3): the incidence increased with shade canopy cover (Fig. 3H) and number of large shade trees (Table 3), but decreased with coffee density (Table 3). There was a weak positive relationship with altitude, even though this relationship was only significant in the separate regression model (Table 3, Fig. 3G). The incidence of Armillaria root rot increased with altitude, shade canopy cover, coffee structure index, and number of large shade trees (Table 3, Fig. 3J-L). The disease incidence decreased with coffee density (Table 3).

### Table 1. Environmental and stand structure variables quantified in each of the sixty study sites. The coffee structure index reflects coffee tree architecture (growth habit) as a result of different management (see the Methods section for details) and the management index captures the common management activities within the different coffee systems (See appendix). Environmental variables are measured within 30 × 30 m plots (except shade trees, which were measured in a 50 × 50 m area), and values in brackets are estimates per hectare.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Min.</th>
<th>Max.</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover (%)</td>
<td>13</td>
<td>83</td>
<td>52</td>
<td>16</td>
</tr>
<tr>
<td>Canopy layers (number)</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>0.8</td>
</tr>
<tr>
<td>Coffee shrub density (&gt;1.5 m) (number/ha)</td>
<td>107 (1189)</td>
<td>1101 (12233)</td>
<td>351 (3900)</td>
<td>178</td>
</tr>
<tr>
<td>Coffee structure index (see Methods section)</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>0.5</td>
</tr>
<tr>
<td>Management index (See appendix)</td>
<td>0.33</td>
<td>1.67</td>
<td>0.77</td>
<td>0.40</td>
</tr>
<tr>
<td>Shade trees &gt;20 cm DBH (number/ha)</td>
<td>5 (20)</td>
<td>43 (172)</td>
<td>22 (88)</td>
<td>9</td>
</tr>
<tr>
<td>Surrounding forest area within 1 km buffer (km²)</td>
<td>0.16</td>
<td>3.22</td>
<td>1.58</td>
<td>0.73</td>
</tr>
<tr>
<td>Proportion of non-coffee shrubs to coffee (%)</td>
<td>0</td>
<td>32</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Altitude (m a.s.l.)</td>
<td>1506</td>
<td>2159</td>
<td>1851</td>
<td>174</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>1</td>
<td>24</td>
<td>11</td>
<td>5</td>
</tr>
</tbody>
</table>

### Table 2. Site-level variation in disease levels and the relative amount of variation in disease levels present among sites and among shrubs within sites (see methods section). Values for coffee leaf rust are based on the mean proportion of leaves with leaf rust averaged across all 16 shrubs per site. Values for coffee berry disease are based on; i) branches with coffee berry disease – mean proportion of number of bearing branches with coffee berry disease and ii) berries with coffee berry disease – mean proportion of berries with coffee berry disease from 16 shrubs per site. Values for coffee wilt disease and Armillaria root rot are based on the proportion of coffee shrubs with their respective disease symptoms per site. For all the four diseases, the proportions are converted to percentages.

<table>
<thead>
<tr>
<th>Diseases</th>
<th>Min. (%)</th>
<th>Max (%)</th>
<th>Mean (%)</th>
<th>Variation among sites (%)</th>
<th>Variation within-site (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coffee leaf rust</td>
<td>0.1</td>
<td>35.1</td>
<td>9.28</td>
<td>12</td>
<td>88</td>
</tr>
<tr>
<td>Coffee berry disease</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i) berries with coffee berry disease</td>
<td>0</td>
<td>45.7</td>
<td>7.50</td>
<td>57</td>
<td>43</td>
</tr>
<tr>
<td>ii) branches with coffee berry disease</td>
<td>0</td>
<td>20.7</td>
<td>3.85</td>
<td>48</td>
<td>52</td>
</tr>
<tr>
<td>Coffee wilt disease</td>
<td>0</td>
<td>5.26</td>
<td>1.47</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Armillaria root rot</td>
<td>0</td>
<td>5.38</td>
<td>0.53</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
Table 3. Summary of the relationship between abiotic and biotic environment and management intensity and incidence and severity of the four major fungal diseases of coffee. Shown are $\chi^2$-values and standard regression coefficients (SC) from the minimum adequate model (except *), as estimated from generalized linear (mixed) models.

<table>
<thead>
<tr>
<th>Response variables</th>
<th>Altitude</th>
<th>Slope</th>
<th>Shade trees &gt; 20 cm (DBH)</th>
<th>Coffee density</th>
<th>Proportion of non-coffee to coffee shrubs</th>
<th>Coffee structure index</th>
<th>Surrounding tree cover (km$^2$)</th>
<th>Surveying date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coffee leaf rust severity</td>
<td>$\chi^2 = 47.38$</td>
<td>$p = 0.001$</td>
<td>$\chi^2 = 5.74^*$</td>
<td>$\chi^2 = 6.68$</td>
<td>$\chi^2 = 63.18$</td>
<td>$\chi^2 = 5.18$</td>
<td>$\chi^2 = 26.53$</td>
<td>$\chi^2 = 0.001$</td>
</tr>
<tr>
<td>SC = -0.64</td>
<td>SC = -0.30*</td>
<td>SC = -0.30</td>
<td>SC = -0.30</td>
<td>SC = -0.30</td>
<td>SC = -0.30</td>
<td>SC = -0.30</td>
<td>SC = -0.30</td>
<td>SC = -0.30</td>
</tr>
<tr>
<td>Berries with coffee berry disease</td>
<td>$\chi^2 = 23.76$</td>
<td>$p = 0.001$</td>
<td>$\chi^2 = 7.03$</td>
<td>$\chi^2 = 0.008$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
</tr>
<tr>
<td>SC = 1.62</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
<td>SC = 0.20</td>
</tr>
<tr>
<td>Branches with coffee berry disease</td>
<td>$\chi^2 = 22.46$</td>
<td>$p &lt; 0.001$</td>
<td>$\chi^2 = 8.81$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
</tr>
<tr>
<td>SC = 1.34</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
<td>SC = 0.64</td>
</tr>
<tr>
<td>Coffee wilt disease</td>
<td>$\chi^2 = 45.09^*$</td>
<td>$p &lt; 0.001$</td>
<td>$\chi^2 = 6.68$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
</tr>
<tr>
<td>SC = 0.28</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
<td>SC = 0.12</td>
</tr>
<tr>
<td>Armillaria root rot</td>
<td>$\chi^2 = 27.60$</td>
<td>$p &lt; 0.001$</td>
<td>$\chi^2 = 9.74$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
<td>$\chi^2 = 0.003$</td>
</tr>
<tr>
<td>SC = 0.43</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
<td>SC = -0.34</td>
</tr>
</tbody>
</table>

*Values from individual regression models.

Co-occurrence patterns of the major fungal diseases

Pearson correlation analyses of the relationship between the different fungal diseases indicated that the four fungal diseases did not co-occur across sites, as evidenced by the weak and non-significant pairwise correlations ($r < 0.22$, $p > 0.085$, see Appendix C: Table C2). Similarly, the correlations between the residual values extracted from the disease models reported in the previous section, which reflect the variation in disease levels remaining after accounting for the environmental and management variables, were all non-significant ($r < 0.12$, $p > 0.34$, see Appendix C: Table C3). However, coffee leaf rust and berry disease co-occurred more frequently on the same shrubs within sites (SC = 0.27, $\chi^2 = 133.9$, $p < 0.001$, see Appendix C: Table C4, Fig. C2).

Discussion

We studied fungal disease communities on Arabica coffee along a management gradient from only little managed wild coffee under a natural forest canopy to intensively managed plantations, within the crop’s native range. All four diseases had high incidence across the 60 investigated sites. However, the incidence and severity of each disease was related to different combinations of environmental (like altitude and shade cover) and management variables along the gradient and did not co-occur more or less often than chance at the same sites. However, within sites, shrubs with a higher severity of coffee leaf rust also had more coffee berry disease and vice versa even if this pattern was weak. Overall, our findings indicate that altitude, canopy cover and management intensity are crucial in driving disease distributions, but that fungal species differ in the direction and strength of their response to these environmental factors.

Variation in disease levels within and among sites

Pathogen species showed strongly divergent multi-scale distributional patterns, despite being present within the same landscape and attacking the same host plant. Coffee leaf rust severity was highly variable among sites, but even more so among shrubs within sites. The large within-site variation in coffee leaf rust may be due to a high sensitivity to the local microclimate (Samnegard, Hambäck, Nemomissa & Hylander, 2014). For example, small-scale heterogeneity in canopy cover is common, and may affect both the microclimate and splash dispersal (Avelino, Willocquet & Savary, 2004). Coffee shrubs close to infected shrubs could also be at a higher risk of receiving spores dispersed by rain, wind and coffee pickers (Waller, 1982), thus creating a within-site spatial clustering.

In contrast to leaf rust, coffee berry disease varied more among sites than among shrubs within sites. One reason may be that coffee berry disease responds to environmental factors that are less heterogeneous at the small scale (Derso & Waller, 2003), or that efficient within-site dispersal results in more uniform infection levels within sites. Importantly, resistance against this disease is present within wild coffee populations. Besides, locally-selected varieties with resistance against coffee berry disease have been released by
Jimma Agricultural Research Center (JARC). Hence, among-site variation may be either a natural phenomenon, or due to some farmers using cultivars that differ in resistance to the coffee berry disease. A promising future avenue for research is to interview farmers about the origin of their coffee plants, as well as characterization of neutral
and adaptive genetic variation among and within sites. The latter approach may also identify valuable genetic material for breeding purposes.

The drivers of disease communities on coffee

When focusing on disease communities on Arabica coffee, we found that the strength and direction of the effect of environmental drivers and management differed strikingly among the individual diseases. In general coffee leaf rust and Armillaria root rot were more common in intensively managed sites, while coffee berry and coffee wilt diseases were more common in the less intensively managed part of the gradient. As a proxy for climate, altitude seemed to be an important driver, but in different directions. Our findings that altitude negatively correlated with coffee leaf rust severity, but positively affected coffee berry disease levels confirm previous studies on coffee leaf rust (Chala et al., 2010) and coffee berry disease (Hindorf & Omondi, 2011). Coffee leaf rust was also more severe under lower shade canopy cover (see also Soto-Pinto et al., 2002). As more open canopies create a warmer temperature and lower humidity, the climatic drivers behind the effect of shade canopy cover may then be similar to those that shape the altitudinal disease gradient. However, under laboratory conditions, coffee leaf rust requires high air humidity or moisture on the leaf surface to germinate and a temperature in the range of 22–28 °C to cause infection and sporulation (Nutman, Roberts & Clarke, 1963; Waller, 1982). Hence, we tentatively suggest that moisture levels are high enough for the rust to thrive in the low altitude and low canopy cover sites investigated by us (c.f. López-Bravo, Virginio-Filho, de & Avelino, 2012), whereas temperature could be the limiting factor at higher altitudes. Dispersal from surrounding areas might play a role for local levels of coffee leaf rust, since there was somewhat higher severity in sites with more tree-cover in the surrounding 1-km buffer.

In our study, both coffee wilt disease and Armillaria root rot increased with altitude and canopy cover, but had higher disease levels at opposite ends of the management gradient, with coffee wilt disease more common in the less managed forest sites and Armillaria root rot more common in intensively managed sites. The affinity of coffee wilt disease to higher altitudes was surprising since it has been known to occur over a wide altitudinal range and has previously been reported as a major problem in lowland areas of coffee production in Ethiopia (Girma, Huluka & Hindorf, 2001). The spread of Armillaria root rot among neighboring shrubs is facilitated by its rhizomorphs that prefer cooler environments to develop (Gezahgne, Coetzee, Wingfield, Wingfield & Roux, 2004; Otieno, Sierra & Termorshuizen, 2003) and this may explain the higher frequency of infection at higher altitudes.

Species may co-occur if they respond to the same environmental variables, i.e., if local conditions fall within the fundamental niche of both species (Chunco, Jobe & Pfennig, 2012). Since all the four diseases we investigated changed in severity along the altitudinal gradient (positive or negative) it could be expected that they would have shown significant co-occurrence patterns across sites (either positive or negative). However, this was not the case implying that the diseases have individual responses in relation to several other drivers, even if they were all partly driven by altitude.

However, our findings indicate that, within a site, shrubs with severe leaf rust infection also had a higher proportion of berries infected by coffee berry disease (and vice versa). Even if this pattern was rather weak, it is suggesting that there could be a direct or an indirect interaction between the two diseases. One possible mechanism accounting for this pattern could be that an infected and subsequently weakened host is more susceptible to infection by another pathogen (Singer, 2010). Interestingly, a very similar case was reported from Costa Rica where coffee leaf rust and the American leaf spot disease (caused by Mycenae citricolor) were inversely driven by altitude, but still had a positive association (Allinne, Savary & Avelino, 2016; Avelino et al., 2018).

Implications for management

Since the four diseases were characterized by their own niches and different, sometimes contrasting relationships with the environment, it is inherently difficult to come up with simple management recommendations for the whole disease community (see Jonsson, Raphael, Ekborn, Kyaminya & Karungi, 2015). Even coffee berry disease, coffee wilt disease and Armillaria root rot, which all increased in prevalence at higher altitudes, did not positively co-vary among the sites, showing that the combination of conditions that favor one species might not favor another. This is an important take home message from this study, which would not have been possible by a series of separate studies focusing each on a single disease.

However, based on our field observations and discussions with farmers, coffee berry disease is perhaps the most problematic in terms of its effect on the harvestable yield and might thus be the species to focus most on (see also Alemu, Adugna, Lemessa & Muleta, 2016; Garedew, Lemessa & Pinard, 2017). On the other hand, coffee wilt disease and Armillaria root rot kill all infected coffee shrubs and therefore cause considerable yield losses. Also, the higher occurrence of coffee wilt disease in less managed forests warrants consideration since it could endanger the in situ conservation of the genetic diversity of coffee (Getachew, Adugna, Lemessa & Hindorf, 2012, 2013). Yet, even if coffee leaf rust is not regarded as a major problem by local farmers...
(personal communication), this may be an underestimation as the infection symptoms are not related to a direct yield loss (Hindorf & Omondi, 2011).

In southwestern Ethiopia, smallholder coffee production usually follows the 'low input – low output' principle (Petit, 2007). At the same time, the farmers’ goals are to increase yield, receive a better revenue at lower costs of production, and stabilize yield among years. Thus, from the farmer’s perspective it is the combined effect of diseases and pests in combination with the amount of invested labor that will matter in the end. However, it is also important to note that shaded coffee systems have other values for the society than direct revenue from berry production. They harbor high biodiversity both at a local scale (Buechley et al., 2015; Schmitt, Senbota, Denich, Preisinger & Boehmer, 2010; Tscharntke et al., 2015) and as part of the landscape (Hylander & Nemomissa, 2008; Shumi et al., 2018; Tscharntke, Klein, Kruess, Steffan–Dewenter & Thies, 2005). Yet, another biodiversity value with these landscapes is the genetic pool of wild coffee. Thus, attempting to approach coffee berry disease problems with resistant coffee genotypes should be done cautiously, since it could ruin the genetic diversity of coffee in its native forests (see Aerts et al., 2013). Future research thus needs to assess to what extent yield and farmers’ revenues trade-off against biodiversity values in this system and if management to reduce the impact of different fungal diseases can modify such relationships. Given these complexities there is much to win by developing nature-based solutions to disease problems, but local farmers might need financial support, for example through certification programs (Gove, Hylander, Nemomissa & Shimelis, 2008; Tscharntke et al., 2015).

Declaration of interest

Authors declare no conflict of interest.

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Supplementary materials

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References


