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RESEARCH ARTICLE

Spatially explicit models predict coffee rust spread in fragmented landscapes

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Abstract
Context Landscape structure influences the spread of plant pathogens, including coffee leaf rust, a fungal disease affecting the coffee industry. Rust transmission is likely affected by landscape structure through the dispersal of wind-borne spores. Previous studies found positive associations between rust incidence and the proportion of pasture cover, suggesting deforestation may facilitate spore dispersal.

Objectives We explored the links between landscape structure and coffee rust by modeling the spread of rust transmission. We investigated how (1) spatial clustering of coffee farms, (2) proportion of landscape deforestation, and (3) clustering of deforestation affects the speed of rust transmission.

Methods We developed a probabilistic model to simulate within-patch and between-patch transmission in simulated and real landscapes. We modeled within-patch transmission using a probabilistic cellular automata model and between-patch transmission using a random walk with spore movement inhibited by canopy cover.

Results Clustering of coffee farms is the primary driver of rust transmission. Deforestation is a secondary driver of rust spread: outbreaks spread more rapidly in landscapes where deforested areas are evenly dispersed throughout the landscape. When applied to real landscapes in Costa Rica, the model yields the same trends as simulated landscapes and suggests increased amounts of coffee near the starting location of the outbreak are correlated with more rapid rust spread.

Conclusions It is essential to consider landscape structure when managing the spread of crop diseases. Increasing the spacing between coffee farms and reducing forest fragmentation in coffee-growing regions can benefit biodiversity conservation and reduce the economic impacts of coffee rust.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-022-01473-1.

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Introduction

Many ecological systems are characterized by their landscape configuration, including natural or anthropogenic habitat fragmentation (Levin 1992; Fahrig 2003). Landscape structure, including the distribution and quality of habitat, affects the connectivity of habitat patches. Changes in connectivity impact various species through changes in habitat patches, patch size, and extinction risk, as well as edge effects (Wiegand et al. 2005; Gavish et al. 2012; Fahrig 2013; Haddad et al. 2015; White and Smith 2018; Riva and Fahrig 2022). One area where landscape structure has been particularly relevant is in the spread of disease (White et al. 2018).

The conversion of native habitat for agriculture and urban development is associated with an increase in infectious diseases (Ellwanger et al. 2020; Gibb et al. 2020). Although evidence remains mixed (Hagenaars et al. 2004; Tracey et al. 2014), previous work suggests that both habitat fragmentation and decreased habitat quality can increase the likelihood of disease spread (White et al. 2018). Plantegenest et al. (2007) suggest there are four landscape-level factors that influence plant pathogen dynamics: (1) landscape composition influences global inoculation pressure, (2) landscape heterogeneity impacts pathogen dynamics, (3) landscape structure affects pathogen dispersal, and (4) landscape properties can induce the emergence of pathogens. Yet, there have been limited efforts to understand mechanistically how landscape structure affects plant disease populations (Cunniffe et al. 2015).

Here we use the plant disease, coffee leaf rust (*Hemileia vastatrix*), as a model system for understanding issues of fragmentation and disease spread. This plant disease infects leaf tissues of cultivated coffee species, leading to defoliation and reductions in vegetative growth, all of which reduce coffee berry yields (Waller 1982). First recorded in 1879, coffee leaf rust is a fungal disease notably recognized for destroying the coffee industry in Sri Lanka, which used to be one of the largest coffee-producing countries in the world. Since the 1970s, coffee rust has spread to the largest coffee-producing regions in the world including Brazil, Mexico, and Colombia. Reports of up to 30–50% losses due to coffee rust in Brazil and Costa Rica, 31% in Colombia, and 16% in Central America make this disease an urgent priority for the coffee-growing industry (Baker 2014; Avelino et al. 2015; McCook and Vandermeer 2015; Zambolim 2016; Cerda et al. 2017).

Transmission of coffee leaf rust spores occurs at two spatial scales. Local or within-patch transmission of spores can occur through the wind (Kushalappa and Eskes 1989), the impact of raindrops of coffee leaves (Rayner 1961a, b; Boudrot et al. 2016), and leaf-to-leaf contact (Vandermeer et al. 2018). For local mechanisms, transmission is thought to decline with increasing distance from the infected source (Vandermeer et al. 2018); therefore a coffee plant with more infected neighbors is more susceptible to infection than a plant with few or no infected neighbors. Regional or between-patch transmission, by contrast, is more likely to be affected by wind patterns and barriers inhibiting wind movement (Becker et al. 1975; Martinez et al. 1975; Waller 1982; Kushalappa and Eskes 1989; Avelino et al. 2015).

While there is a vast amount of knowledge on the epidemiology and environmental drivers of coffee rust, the impacts of landscape structure on coffee rust spread remain poorly understood (but see Vandermeer and Rohani 2014; Vandermeer et al. 2015). Local context such as shade cover and proximity to pasture has been shown to be positively correlated with coffee rust incidence, highlighting the need to investigate how habitat fragmentation due to deforestation influences the spread of coffee rust (Avelino et al. 2012). Yet, few studies have focused on how landscape patterns may influence the spread and infection rates of coffee rust. The relative lack of landscape-level research may be due to the difficulty in collecting data across such a large scale. However, recent advances in computing power facilitate the use of simulation models to address processes occurring at the landscape scale. Here, we use simulation models to investigate how landscape-level composition and configuration influence the spread of coffee rust.

We hypothesize that the windborne dispersal of rust spores is facilitated by landscape composition and configuration. Specifically, we examine the effects on disease transmission from the spatial clustering of coffee farms (defined as the aggregation of individual coffee farms in the landscape), the proportion of deforestation within the matrix, and the degree to which deforested areas are scattered in space (Fig. 1). We predict that rust spores will disperse more readily through landscapes with high coffee clustering and deforestation levels; resulting in

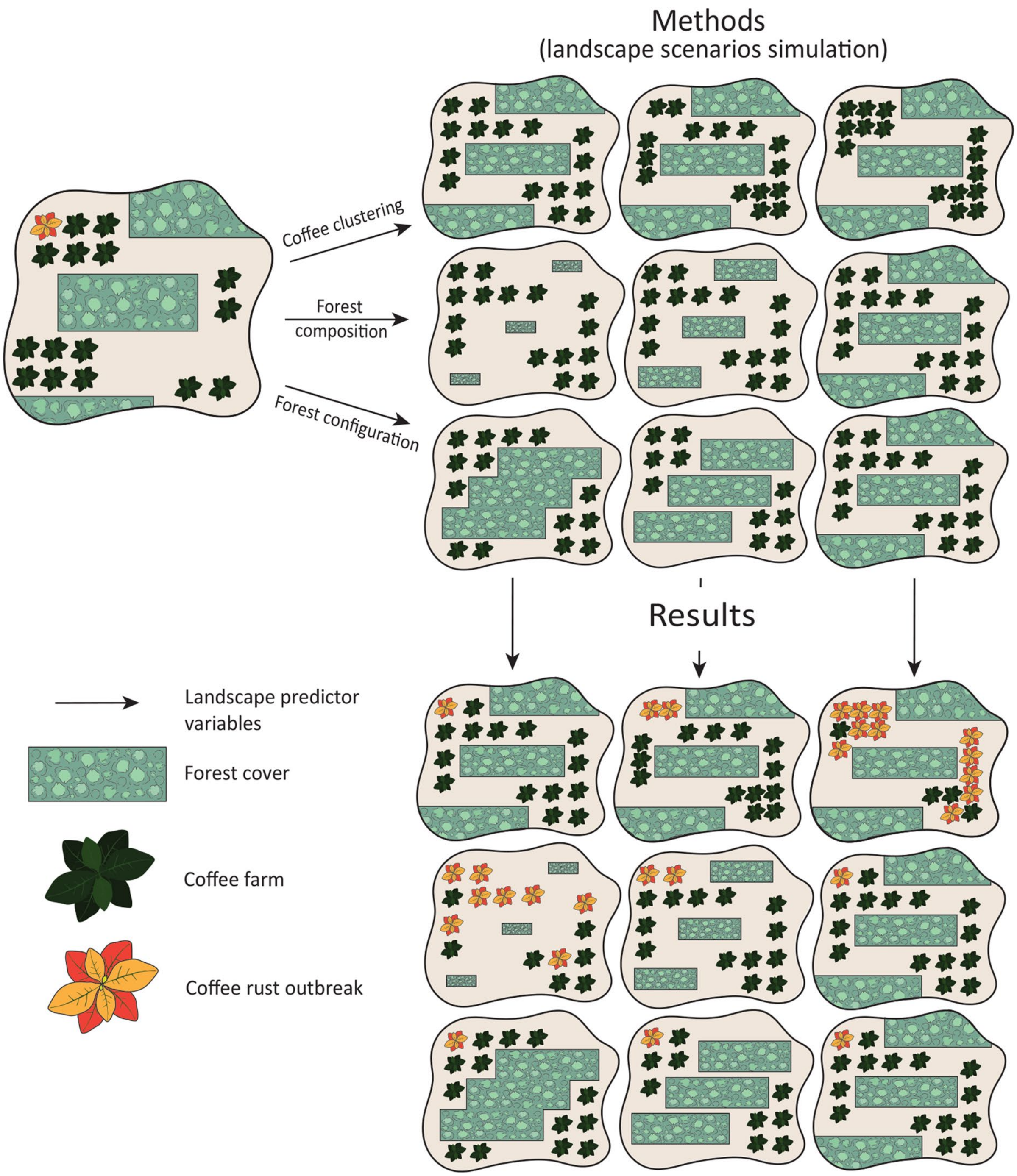

Fig. 1 Graphical illustration of our methods and results. We simulated landscapes based on differing levels of landscape structure predictor variables from low to high (reading left to right). Results show how each landscape predictor variable influences the spread of coffee rust outbreaks within each simulated landscape

a higher incidence of coffee rust in landscapes that exhibit these characteristics. In addition to the simulated landscapes, we used the model to compare the potential for rust outbreaks in two regions in Los Santos, Costa Rica.

Table 1 Parameter values for simulated landscapes

Parameter	Values
Coffee clustering	0.1, 0.2, 0.3
Proportion of deforestation	0.15, 0.3, 0.45, 0.6, 0.75
Clustering of deforestation	1, 2, 3, 4, 5

Methods

Landscape simulation

We modeled landscapes using two 100 × 100 rasters constructed using the package NLMpy (Oliphant 2006) in Python 3.7.1 (Python Software Foundation 2018). Rasters had reflective boundaries and included a 10-cell buffer around each edge to mitigate boundary effects (Keane et al. 2006; Koen et al. 2010). The first raster in each landscape was a binary raster of coffee/not coffee, where each coffee cell represented 1 coffee farm. The coffee raster was constructed using the NLMpy function randomClusterNN (Etherington et al. 2015) which is an adaptation of the modified random cluster algorithm (Saura and Martınez-Millan 2000). The algorithm creates a series of random clusters taking on values between 0 and 1, with the user defining (1) the proportion of cells in the array that are randomly assigned to form clusters, and (2) the neighborhood rule that affects the size and directional bias of the clusters. After the initial clusters are formed, the algorithm assigns values to the remaining cells using nearest-neighbor interpolation.

We assigned a Moore neighborhood rule to all coffee rasters in the simulation. We defined the proportion of cells assigned to clusters as a parameter ranging from 0.1 to 0.3 (Table 1). After generating the initial landscapes, we reclassified the coffee rasters using the NLMpy function classifyArray (Etherington et al. 2015), weighted so the final landscapes were composed of approximately 25% coffee (represented by 0's) and 75% not-coffee (represented by NaN values—essentially empty cells). The parameter controlling the proportion of cells assigned to clusters affected the degree of aggregation in the reclassified rasters:rasters that were generated using a value of 0.1 resulted in small clusters that were evenly distributed throughout the landscape, whereas rasters generated using a value of 0.3 resulted in larger patches that were not evenly distributed (Fig. S1).

The second landscape aspect we modeled represented the surrounding matrix and "mirrored" the coffee raster (i.e. cells containing coffee were empty in the matrix raster). Values in each matrix cell represented canopy density. The proportion of the array consisting of deforested cells, or cells with a canopy density less than 30%, ranged from 0.15 to 0.75 (Fig. S2). Although there is some debate surrounding the minimum canopy cover required to declare an area "forested" (Putz and Redford 2010), we chose 30% based on the implementation guidelines of the Clean Development Mechanisms of the Kyoto Protocol (UNFCCC 2006). We controlled the aggregation of deforested cells with a parameter taking values from 1 to 5, with 1 being the most clustered and 5 the most dispersed (Table 1; Fig. S3).

We generated 50 replicate landscapes for each combination of parameter values for a total of 3750 simulations. We initialized rust infection by randomly selecting one coffee cell in each simulated landscape and changing the value of the cell to 1.

Modeling rust transmission

We modeled transmission of coffee rust through the simulated landscapes using a two-step process linked by two transition processes (Fig. S4). The two processes in our model reflect differences in rust dispersal mechanisms at the local (within-patch) and regional (between-patch) scales. We modeled local transmission using a stochastic cellular automata model (Wolfram 2002), in which the probability of infection in the focal cell at time $t+1$ is determined by $p \sim Beta(N, 8\text{-}N)$ where N is the number of infected cells in the focal cell's Moore neighborhood. Because the model assumes that local spread only occurs via transmission between immediate neighbors, a cell with no infected neighbors had a probability of infection $p = 0$.

After modeling local spread, the model transitioned to regional spread when all infected coffee cells at the edge of a cluster released 1 spore into an adjacent, randomly selected matrix cell in the infected cell's Moore neighborhood. After new spores were released, all spores moved throughout the landscape using a modified random walk in which canopy cover was assumed to inhibit spore movement. At the beginning of the walk, all spores were assigned equal "movement values" which determined how far the spore could move during the time step. Each movement then consisted of a three-step process: (1) the destination, or target cell, was randomly selected from the focal cell's Moore neighborhood, (2) the spore moved into the target cell and the percent canopy cover in the target cell was subtracted from the movement value, and (3) if the remaining movement value was greater than 0, the process was re-initialized so the spore could move again. For example, if a spore started with a movement value of 1 and moved into a cell with a canopy cover of 0.8, the movement value would change to 0.2 and the spore would move again. If the spore then moved into a cell with a canopy cover of 0.3, the movement value would change to − 0.1, and the spore would not move again until the movement value was reset at the next time step.

Upon completion of the simulated walk, each spore adjacent to an uninfected coffee cell infected the cell with a probability of success set at 0.5. This value is somewhat arbitrary as infection rates are heavily influenced by other processes we did not specify; specifically the coffee variety and environmental factors (van der Vossen et al. 2015; Ward et al. 2017). However, we chose 0.5 for model simplicity. If a spore was adjacent to multiple uninfected cells, the target cell was selected randomly. Spores that successfully infected a cell were removed from the simulation. We repeated this four-part process for 1000 time steps per simulated landscape.

Analyses

We calculated the mean rate of spread, defined as the average number of new infections per time step, of each replicate. We calculated the mean rate of spread rather than traditional metrics such as the proportion of the landscape that is infected due to size and composition differences between the simulated and real landscapes. Assuming the distribution of the rate of spread followed a gamma distribution, we estimated the shape and rate (α and β) parameters of the distribution using the R package fitdistrplus (Delignette-Muller and Dutang 2015; R Core Team 2020). Using the estimated values of these parameters, we calculated (1) the expected value of the distribution, (2) skewness, and (3) kurtosis, which describes the "tailed-ness" of the distribution. We also compared the maximum rate of spread of each replicate and performed these calculations with (1) all simulation replicates pooled, (2) replicates separated by clustering value, and (3) replicates separated by all parameter values. We evaluated associations between deforestation, dispersion, and the properties of the gamma distribution using Spearman's ρ. Correlations of $\rho > 0.4$ *or* $\rho < -0.4$ were considered important. We did not use p-value significance testing to evaluate our results, as increasing the number of simulations can artificially increase sample size and confound significance tests (White et al. 2014).

Application to real landscapes

For our real landscapes, we used two areas of 97 km^2 located in Los Santos, a mountainous region in Central Costa Rica known for its high-quality and altitude coffee. The maps include land-use classification from 2015 high-resolution Ikonos images (1:5000) done by the Ecosystems Modeling Lab at The Tropical Agricultural Research and Higher Education Center (CATIE). Coffee in this region is usually grown in small farms—mean size is 5.45 ha—ranging from 1000 to 2300 m.a.s.l. in altitude. The main varieties of *Coffea arabica* produced are Caturra and Catuaí, which are highly susceptible to coffee leaf rust. More than 80% of farmers in Los Santos reported having problems with coffee rust, and 37% changed coffee varieties due to it and other diseases (Viguera et al. 2019).

We applied our model to two rasters that represented two locations within the greater Los Santos region, hereafter called Landscape 1 and Landscape 2. Raster cell size was approximately 1.5 km^2 in each raster. Coffee was the dominant land cover class in each raster, representing 52% and 54% of Landscapes 1 and 2, respectively (compared to 36% coffee in the simulated landscapes). Forest and pasture were also common land cover classes in each landscape (17.3% and 15.4% in Landscape 1, 21.0%, and 10.8% in Landscape 2).

Landscape 1 also contained a large body of water in the southern portion of the raster.

We compared coffee clustering, the proportion of the matrix that is deforested, and the dispersion of deforestation between the two real landscapes in Los Santos. We defined coffee clustering using He's aggregation index (He et al. 2000), of which Landscape 1 had an aggregation index of 85.1 and Landscape 2 an aggregation index of 87.0. We used these values and the proportion of forest cover in the landscape to predict outcomes based on the results of the simulated landscapes. We initialized rust infection and ran the simulation described above 50 times per landscape for 100 total simulations. We calculated the mean rate of spread, defined as the average number of new infections per time step, of each replicate to facilitate comparisons with the simulated landscapes.

To evaluate how the starting location of the outbreak affected the mean rate of rust spread, we drew 50×50-cell square buffers around the starting cell of each simulation. Within this buffer, we reclassified all non-coffee and non-forest cover types, including human settlements, shrubland, and open water, as "other." We compared the land cover composition within this buffer to the mean rate of spread and evaluated the strength of the correlations using Spearman's ρ. For both of these analyses, a value of $\rho > 0.4$ and $\rho < -0.4$ were considered important.

Domain effects and spatial autocorrelation in the real landscape rasters may influence the outcome of the model. We tested for domain effects, specifically distance to the landscape boundary, by testing for correlations between distance from the initially infected cell to the landscape boundary and rate of spread using Spearman's ρ. We tested for spatial autocorrelation between the initially infected cell and outbreak size using Moran's I (Moran 1950). Similarly to previous tests, values of ρ and Moran's I between -0.4 and 0.4 were not considered important relative to the landscape metrics of interest, and we did not report p-values because they are readily manipulated by increasing the number of simulations.

Results

Simulated landscapes

The average rate of spread across all parameter values ranged from 0 to 2.08 new infections per time step (Fig. 2). The estimated parameters of the full distribution were estimated at $\alpha = 0.173$ and $\beta = 0.780$. These values correspond to an expected value $E(x) = 0.221$, a skewness of 4.813, and kurtosis 34.759.

All four metrics varied among coffee clustering values. The expected value and maximum rate of spread were greatest in landscapes with high clustering but did not appear to differ between low and moderate clustering values (Fig. 3a, b). Conversely, the distributions of outcomes at high clustering values were less skewed and had lower kurtosis ("tailedness") than distributions at low or moderate clustering values (Fig. 3c, d).

We did not find consistent effects of deforestation and dispersion within clustering values, but at the highest value of coffee clustering, the maximum infection rate tended to be higher in landscapes where deforestation was highly dispersed ($\rho = 0.486$, Fig. 4).

Real landscapes

The rate of rust spread in the two landscapes was similar (Fig. 5), although the mean rate of spread in Landscape 2 was marginally higher. The geographic location of the initial infection appeared to influence the rate of rust spread, especially in Landscape 1 (Fig. 6). Within-landscape differences in the rate of spread may be influenced by land cover composition around the starting location of the outbreak (Figs. 7, 8): the rate of spread in Landscape 1 was positively correlated with the proportion of coffee in a 50×50 cell buffer ($\rho = 0.790$) and negatively correlated with the proportion of cover types categorized as "Other"

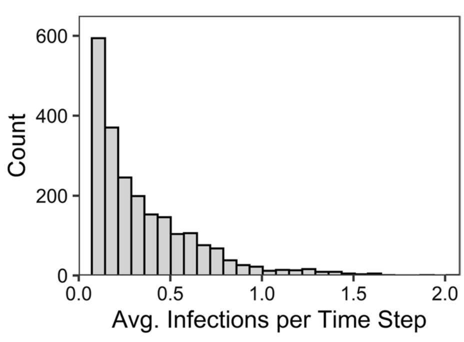

Fig. 2 Distribution of model outcomes across all parameter combinations. Assuming the data follow a gamma distribution, the expected value is 0.221, the skewness 4.813, and the kurtosis is 34.759

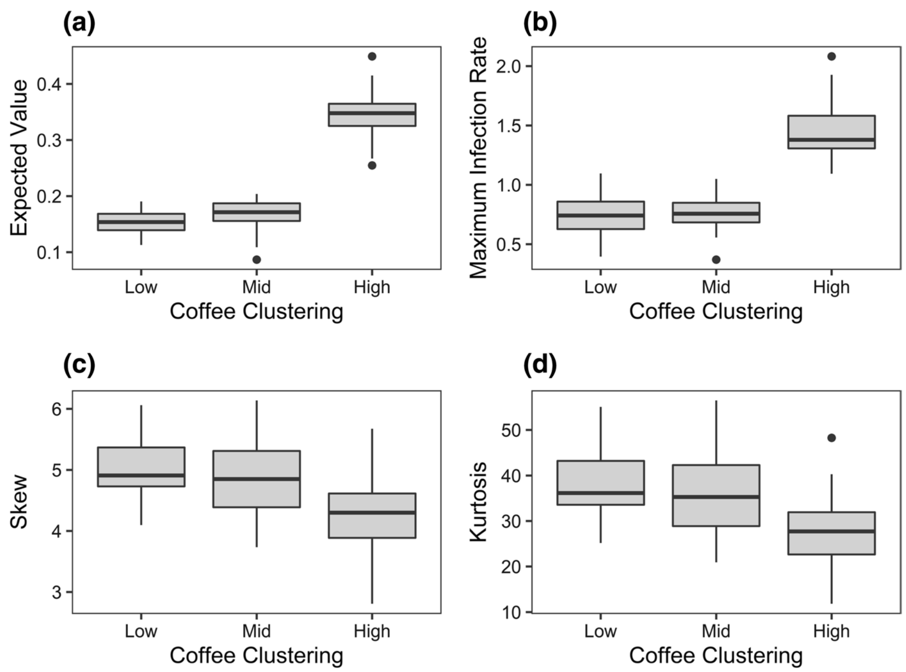

Fig. 3 Different values of coffee clustering yield distributions of rust prevalence that vary in shape. Simulations in which coffee was highly clustered resulted in distributions with a greater expected value (i.e., typical rate of spread) (**a**), and a greater maximum rate of spread (**b**). High clustering of coffee also resulted in distributions that were less right-skewed (**c**) and had narrower tails (**d**)

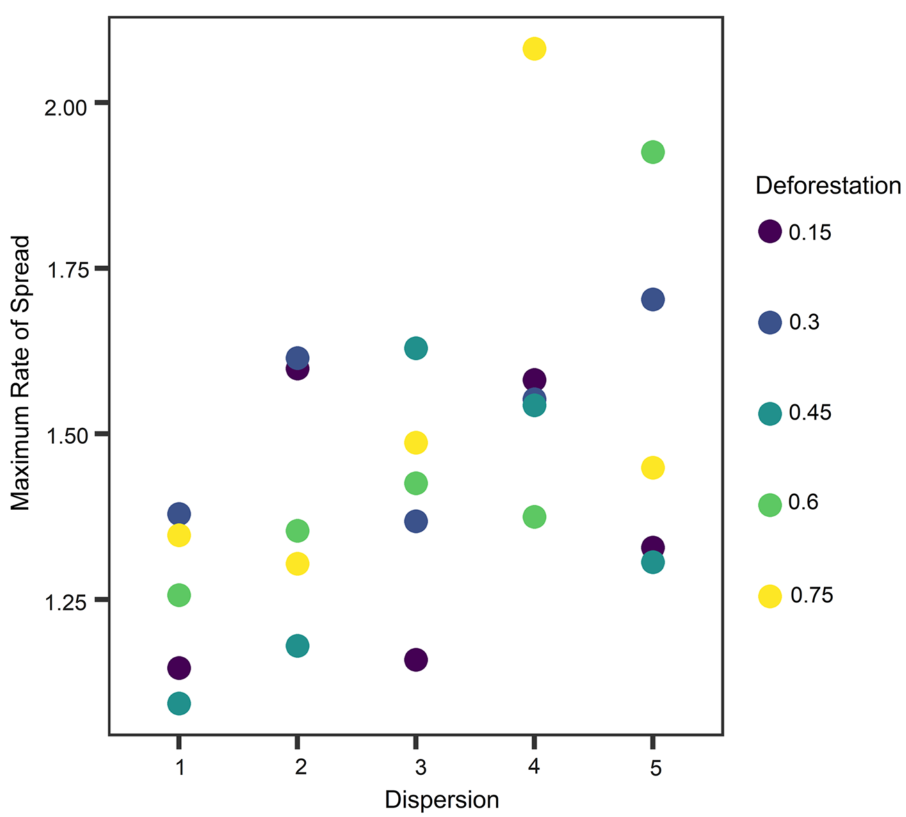

Fig. 4 Effects of dispersion at the highest value of coffee clustering. When deforested areas are dispersed more evenly throughout the landscape, the maximum rate of spread tends to be higher ($\rho = 0.486$)

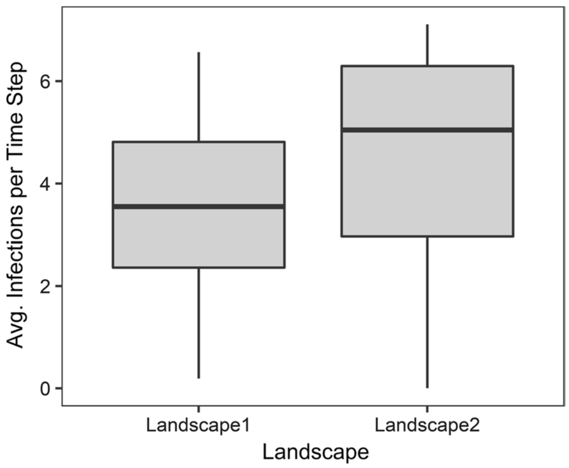

Fig. 5 Mean new rust infections per time step in the two real landscapes

(ρ=-0.804). However, these patterns were not present in Landscape 2 (ρ=0.106 and $\rho = -0.144$, respectively).

Distance to the landscape boundary did not appear to influence the mean rate of spread in Landscape 1 (ρ=0.053) or Landscape 2 ($\rho = -0.338$). The mean rate of spread also did not appear to be spatially autocorrelated in Landscape 1 (I=0.233) or Landscape 2 (I=0.173).

Discussion

Our results suggest that the spatial clustering of coffee farms is the main driver of rust spread (Figs. 3, 7). When coffee farms are clustered in the landscape, the distance to the nearest uninfected farm decreases, allowing spores to quickly reach and infect new areas. Similarly, our landscape simulations indicate that aggregating coffee farms at the local scale (e.g. within-patch) is a key driver of rust spread, and consequently, an important factor to consider when managing coffee rust (Fig. 3). The real landscapes were composed of a much larger proportion of coffee than the simulated landscapes, and the model subsequently yielded higher rates of spread in the real landscapes. Increasing the number of coffee farms around the starting location of the outbreak typically resulted in higher rates of spread, particularly in Landscape 1 (Fig. 7). While deforestation was not a predictor of rust spread in our real landscapes and only played a small role in the simulated landscapes (Fig. 4), landscapes in which forest is replaced with coffee will likely have larger outbreaks due to an increase in host availability.

Due to the potential for long-distance dispersal of windborne spores, individual management strategies are insufficient for managing many fungal diseases. For instance, within-farm management tactics, such as host removal through culling or planting resistant varieties, fail to contain epidemics because they

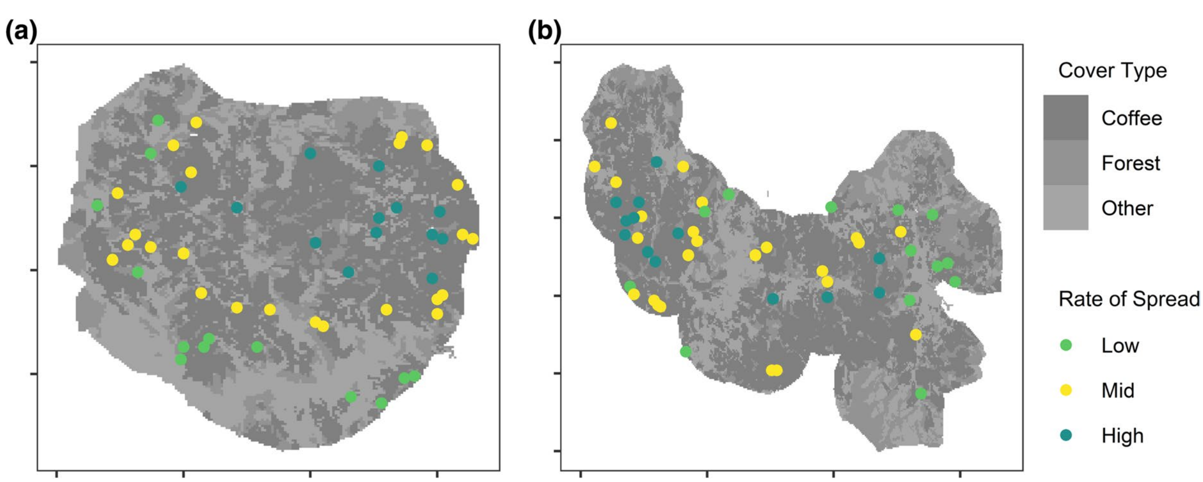

Fig. 6 Starting locations of rust outbreaks in Landscape 1 (**a**) and Landscape 2 (**b**). Colored points denote the quantile for the mean rate of spread; "Mid" indicates the middle two quantiles. Gray cell colors denote land cover type

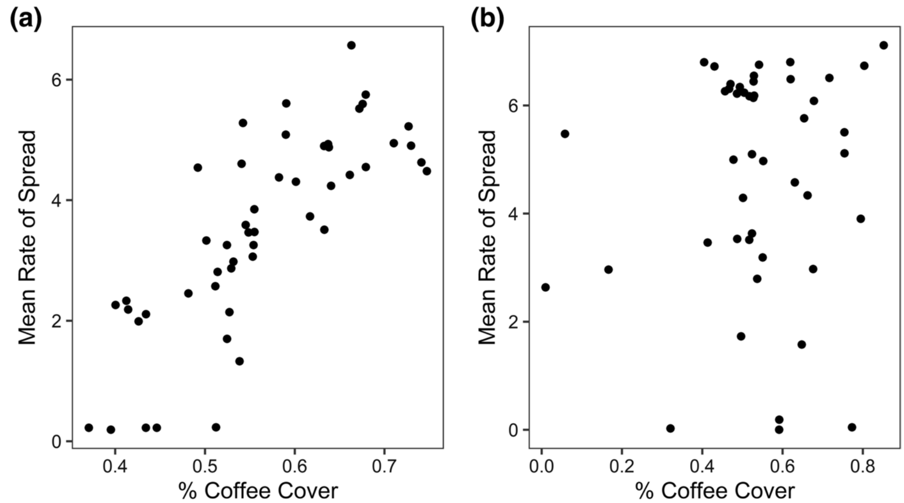

Fig. 7 Correlations between percent coffee cover surrounding the starting locations of outbreaks and rate of rust spread. Coffee cover was positively correlated with the rate of spread in Landscape 1 (**a**, $\rho = 0.790$) but not Landscape 2 (**b**, $\rho = 0.106$)

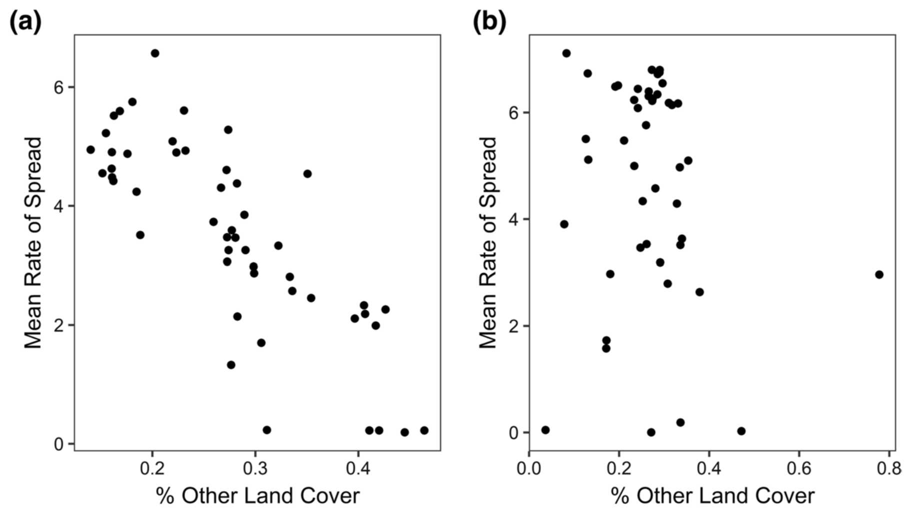

Fig. 8 Correlations between the percent of "other" land cover surrounding the starting locations of outbreaks and the rate of rust spread. "Other" land cover was defined as anything other than coffee or forest, including human settlements, shrubland, and open water. Other cover types were negatively correlated with the rate of spread in Landscape 1 ($\rho = -0.804$) but not Landscape 2 ($\rho = -0.144$)

underestimate the spatial scale of the outbreak (Gilligan 2008). It is possible that high-profile failures to contain plant disease outbreaks, such as sharka (Rimbaud et al. 2015) and citrus canker (Irey et al. 2006), are due to implementing local, reactive strategies rather than a landscape-level approach (Gilligan et al. 2007; Fabre et al. 2019). Our study suggests that individual actions would be particularly ineffective in highly connected landscapes (Fig. 3), where coffee farms are highly aggregated. This finding reflects previous studies regarding disease transmission and landscape modality (Macfadyen et al. 2011). Landscape characteristics of the matrix surrounding farmland, specifically deforestation, can facilitate or inhibit disease spread (Fig. 4), demonstrating a need for management strategies that address processes occurring at multiple but also larger scales (Amico et al. 2020).

Understanding the socio-ecological factors involved in the spatial configuration of farms is crucial to support landscape-level actions that reduce susceptibility to crop diseases. The majority of the coffee in the world is produced on small farms of less than 10 hectares (Jha et al. 2014). Therefore, coffee-growing landscapes are composed of several landowners where cooperation becomes critical for managing coffee rust outbreaks at the regional level. Communication among neighboring farmers may help monitor crop diseases and exchange management information to contain the spread of coffee rust.

In Mexico, Valencia et al. (2015) found that coffee farmers incorporate external knowledge from NGOs and government agencies into their resource management decisions. If cooperation among farmers includes spatial configuration of farms as another factor, this could implement landscape-level approaches to decrease rust spread like minimizing coffee clustering and facilitating community-based reforestation efforts in non-cultivated areas. Examples of cooperation among farmers have been documented for the management of plant diseases such as cassava brown streak disease and Huanglongbing (Bassanezi et al. 2013; Legg et al. 2017). Coordinated management is thought to be most successful among farmers and their immediate neighbors, but at larger spatial scales, competing interests and values may hinder collective management strategies (Sherman et al. 2019). Therefore, an integrative approach that incorporates on-farm, neighborhood, and landscape management strategies may serve as a productive way for farmers, land managers, and government officials to collectively manage coffee rust (Amico et al. 2020).

While spacing out coffee farms may be one solution to prevent rust outbreaks, it may not be a feasible option for farmers with limited space or resources. Alternatively, a collective of individual management actions that are based on farmer decisions may help limit coffee rust spread and thus reduce the chances of outbreaks at the landscape level. For instance, the addition of shade trees in our case study region of Costa Rica, such as banana or plantain (*Musaceae* family), *Erythrina poeppigiana* (also known as poró), and leguminous *Inga* spp. are commonly planted in between rows of coffee and around plots as a method to mitigate the spread of coffee rust (Perfecto et al. 1996; Romero-Alvarado et al. 2002; Albertin and Nair 2004). Shade trees have been shown to reduce spore dispersal by altering winds and providing canopy shade cover, protecting coffee from infection by spores (Avelino et al. 2004; Boudrot et al. 2016; Gagliardi et al. 2020, 2021). Studies that address preventative actions taken by farmers in response to coffee rust outbreaks have noted that shade trees provide an important service for coffee rust management (Soto-Pinto et al. 2002; Narayana 2013; Valencia et al. 2015). To some extent, this type of individual management action offers farmers a way to directly regulate coffee rust at the farm level, but it may not be enough considering the complex interaction between rust transmission and the surrounding landscape.

Based on our results and the results of previous work, it is likely that consideration of spatial arrangement at multiple scales is needed for effective rust management. Hajian-Forooshani and Vandermeer (2021), for example, compared simulated coffee rust spread at the farm level following a simple null model to a network model from empirical data to understand the spatial structure of coffee rust dynamics. Complementary to our results, they found that the spatial arrangement of coffee plants within a farm plot influences the probability of coffee rust outbreaks. Together, the results from our study and results from Hajian-Forooshani and Vandermeer (2021) suggest avoiding high clustering of coffee farms at the landscape scale and uniform spacing of plants at the plot scale to decrease the spread of coffee rust. Thus, when an opportunity to restructure the spatial configuration of a coffee-growing region arises (i.e., replacing coffee plants, buying land for coffee farming, or after a regional disease outbreak, Valencia et al. 2018), incorporating multi-scale approaches to decrease coffee rust spread is important.

Spacing out coffee farms could mean less harvestable area, resulting in a trade-off between farmland extension and the risk of rust outbreaks and rust spread. Additionally, deciding the location of new farms or where farmers get to replant plots highly depends on the economic position of the farmer and this could lead to biased decisions. However, it could also promote opportunities for land reparations. Finding the threshold for these trade-offs or the mechanisms of collective actions or landscape planning were beyond the scope of this study, but are crucial next steps.

Landscape planning and management go hand in hand with collective actions to control crop pests and diseases (Brévault and Clouvel 2019; Vilchez-Mendoza et al. 2022). The homogenization of coffee landscapes, primarily through the clearing of forested areas, has been previously linked to coffee rust outbreaks and continues to present major challenges for disease control (Avelino et al. 2004, 2006; Boudrot et al. 2016; Perfecto et al. 2019). To this end, deforestation, and thus the loss of shade in forested systems, can facilitate the dispersal of rust spores by allowing wind gusts to infiltrate coffee canopies (Perfecto et al. 2019). Our results agree with these mechanistic explanations for the spread of coffee rust within a simplified-homogenous landscape as high levels of clustering and deforestation resulted in a more rapid spread of coffee rust infections. Thus, efforts to undo the effects of landscape homogenization through conservation and reforestation practices may serve as an effective approach to managing coffee rust at the landscape level.

The relative simplicity of our model allows us to focus on landscape effects without having to filter through "noise" created by other environmental processes. However, this simplicity comes with the disadvantage of omitting a handful of factors that may influence how well our model reflects reality. Our model does not include the added complexity of agroforest systems or the direct effects of abiotic conditions such as wind, rainfall, sunlight, and humidity, all of which are known to affect rust transmission and germination (Kushalappa and Eskes 1989; Merle et al. 2020). Wind, in particular, is thought to be the primary mechanism driving landscape-level dispersal of rust spores in monoculture coffee systems (Boudrot et al. 2016). By omitting wind, it is likely our model underestimates the importance of deforestation as a driver of landscape-level prevalence. Additionally, our model treats infection as a binary: a coffee farm is either fully infectious or fully healthy. In reality, the severity of infection within farms and within plants is more of a gradient and may influence the rate of spread by influencing the number of spores that are released from an infected plant (Kushalappa and Eskes 1989). We also do not include environmental variability, such as seasonality, extreme events, or long-term changes including climate change (Pham et al. 2019; White and Hastings 2020). Despite these limitations, our model successfully outlines broad patterns of rust spread and the landscape factors influencing outbreaks, setting the stage for future work.

Conclusions

Our results have important implications for coffee rust landscape management practices. Specifically, our findings suggest that coffee-growing regions should focus on cooperative management in addition to individual practices to reduce coffee rust prevalence. Regionally, reforestation projects and landscape management decisions should consider that landscapes with lower coffee cover tend to have a lower prevalence of coffee rust and are more resistant against outbreaks. Land-use decision-makers should consider that the exact degree and location of deforestation matters for disease outbreaks, as higher dispersion of deforestation seems to lead to outbreaks that spread more rapidly. Given that our study only focused on modeling coffee rust transmission at the farm to landscape scale, further efforts to incorporate additional scales, such as plant to plot to farm to landscape, may allow for a better grasp of transmission dynamics and subsequent management actions (Hajian-Forooshani and Vandermeer 2021). Therefore, reducing landscape homogenization and deforestation at multiple scales is a priority. Additionally, it will be vital to estimate the socio-economic trade-offs between reducing coffee farmland to reduce rust spread and the economic impact to farmers, as well as finding thresholds in the spatial configuration between coffee and forest areas to prevent rust outbreaks.

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Author contribution EMB, NA, and EMB contributed equally to study conception, design, and wrote the first draft of the manuscript. EMB wrote all code for simulations and data analyses. NA obtained real landscape data. All authors read, revised, and approved subsequent drafts of the manuscript.

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Data availability Not applicable.

Code availability All code and model outputs are archived on Zenodo at https://zenodo.org/record/6760264#.Yrm2o3bMJdg.

Declarations

Conflict of interest The authors declare no competing interests.

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