

A multi-scale approach to study palm-weevils in a tropical agroecosystem

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Abstract

Context

The recent phytosanitary crisis caused by the stem borer weevils *Dynamis borassi* and *Rhynchophorus palmarum* in peach palms (*Bactris gasipaes*) seriously affected the economy of local families in Colombia. To understand the possible ecological mechanisms favoring the pest, the weevil-palm system needs to be studied from a multi-scale perspective.

Objectives

We evaluated the combined effects of agricultural management, landscape, topography, soil, and climate variables on infestation levels of peach palm caused by the weevils *D. borassi* and *R. palmarum* in the Colombian southwest to understand underlying ecological drivers of the current phytosanitary crisis.

Methods

The palm infestation levels (response variable) and local agronomic practices were recorded in 32 sites across Colombia's Pacific, Andes, and Amazon natural regions. For each peach palm crop, landscape variables were estimated from classified Sentinel-2 images, soil variables were extracted from the Soil Grids 250 m database, and climate variables were extracted from the CHIRPS and CHIRTS databases. Explanatory variables were analyzed using Generalized Linear Models and Partial Least Squares-Generalized Linear Models.

Results

Landscape variables, specifically the number and shape of non-forest patches, had a greater influence on peach palm infestation levels than other environmental variables, possibly related to the decrease in the density of *Oenocarpus batatua*, the natural palm host for *D. borassi*, leading it to switch to the peach palm.

Conclusions

A multi-scale approach of the weevil-palm interaction enabled us to identify an ecological mechanism that has not been proposed before. Our recommendation for families depending on the palm is to design palm management with a landscape perspective that considers the conservation of alternative hosts for the weevils in agroforestral plots.

Introduction

The first studies on pest-plant interactions and efforts to mitigate damages to plants came from temperate environments and they have traditionally been limited to a plot or small area of crop (e.g., Barnes 1932). Later, variables influencing pest-plant communities at larger scales, such as landscape composition and configuration (Kruess and Tscharntke 1994; Bianchi et al. 2006), topography, and climate (Davis et al., 1996) were incorporated in the study of these interactions. Including variables at scales larger than a plot enabled understanding ecological mechanisms of pest persistence that could not be detected at the scale of a plot. For example, by incorporating a landscape perspective Kruess and Tscharntke (1994) showed that high abundances of a pest in a plot were correlated to a high degree of isolation of the plot, which prevented natural enemies from maintaining viable populations there.

The influences of variables operating at large scales, such as climate, land use, and invasive species on pest-plant interactions are part of global changes that result from the influence of each driver operating alone or in combination with others (Scherer et al. 2000, Sage 2020). For that reason, multi-scale approaches have been useful to study pest-plant interactions in the context of global change (e.g., Villa et al. 2020). While most of our understanding of pest-plant interactions at multiple scales have been built on lines of evidence from temperate environments, fewer studies have tested the validity of those mechanisms for explaining pest-plant interactions in the tropics. Tropical agroecosystems have more stable annual temperatures in comparison with temperate regions, but climate variables may strongly interact with local characteristics and with soil and landscape at large spatial scales (Hilje et al. 2002). In addition, global changes may have different impacts on natural enemy, pest, and plant species (Wagner et al. 2021), and latitudinal influences on these differential impacts remain unclear. For instance, some evidence from temperate environments demonstrates that pests may be negatively impacted by climate change (e.g., Lombardero Díaz et al. 2021), but extreme

environmental climatic events have been shown to lead to pests outbreaks in the subtropics (e.g., Seaton et al. 2015). In a changing world, we need to understand to what degree outbreaks are driven by emerging pests that are able to exploit resources that are newly available after extreme environmental events (Skendžić et al. 2021; Nyamukondiwa et al. 2022), and to evaluate these mechanisms in tropical environments.

Previous research in the tropics have shown a combined contribution of agricultural practices, landscape, and climate on infestation or pest abundance in cassava, coffee, maize, potato, tree, and palm crops (Backlund 2012; Parsa et al. 2012; Poveda et al. 2012; Tsafack et al. 2013; Midega et al. 2014; Jonsson et al. 2015; Baguma et al. 2019; Medeiros 2019; Soti et al. 2019). In particular, a limited number of multi-scale studies have been made to understand the interaction of weevils and cultivated palms. For instance, infestation of oil palms by *Rhynchophorus phoenicis* in Uganda was mainly correlated to distance to natural vegetation cover and to the season, but not to other climate variables (Baguma et al. 2019). In another study in Oman, the attack of *R. ferrugineus* on date palms was related to the age and height of the palm (Azam et al. 2000). Finally, an effect of distance to natural vegetation was relevant to explain predation on “dummy caterpillars” in oil palm in Indonesia (Nurdiansyah 2016). In sum, evidence suggests that including agricultural practices, landscape, and climate in multi-scale studies may be critical to explain pest-palm dynamics in some cases.

The recent phytosanitary crisis in peach palms (*Bactris gasipaes*) in Colombia (Gaviria et al. 2021) is an opportunity to understand an emerging pest in tropical ecosystems using a multi-scale approach. Peach palms are cultivated mainly in the Colombian southwest, an area with a complex orogeny and high heterogeneity in agricultural practices and soil, landscape, and climate characteristics (Rangel-Ch 2015). The phytosanitary problem results from the interaction between the palm weevils *Dynamis borassi* and *R. palmarum* and the palm, whose stem and inflorescences are damaged as a result of the weevil larvae activity (Pardo-Locarno et al. 2016; Vásquez-Ordóñez et al. 2020; Gaviria et al. 2021). *Dynamis borassi*, the emerging palm pest, initiates the damage by attacking unopened inflorescences of the palm and subsequently tunneling the inflorescences petioles towards the stem (Gaviria et al. 2021). These lesions attract *R. palmarum*, which also feeds on the stem. The levels of infestation caused by these weevils are variable among and within ecoregions in the Colombian southwest (Gaviria et al. 2021), but drivers shaping these infestation spatial patterns are still not clear. In addition, a recent study in forests close to peach palm fields in the Colombian Central Pacific demonstrated that *D. borassi* thrived exclusively on the native *Oenocarpus bataua* palms (Bautista-Giraldo et al. 2020). Furthermore, in that region, the abundances of *D. borassi* and *R. palmarum* were contrasting between two distant locations (Gaviria et al. 2021) where the abundance of inflorescences of *O. bataua* (Bautista-Giraldo et al. 2020) and levels of forest conservation were similarly contrasting. These lines of evidence suggest that the new *D. borassi* may have switched from *O. bataua* to peach palm and the underlying ecological mechanisms need to be understood.

In this study, we evaluated the combined effects of agricultural management, landscape, topography, soil, and climate variables on infestation levels of peach palm caused by the weevils *D. borassi* and *R. palmarum* in the Colombian southwest to understand underlying ecological drivers of the current phytosanitary crisis. We determined infestation levels of the palm in 32 sites located in three ecoregions of the country.

Materials and methods

Ethics Statement

The Ministry of Interior in Colombia confirmed that a priori consultation of communities for developing the present investigation was not necessary. The ethical committee of the Universidad del Valle gave the endorsement for studies with flora and fauna. All subjects gave their informed consent for inclusion before they participated in the study. The study was conducted in accordance with the Declaration of Helsinki.

Study site

The study was conducted in 32 localities of peach palm production in three ecoregions of Colombia (Rangel-Ch 2015): the Amazon, the Andes, and the Pacific. Eighteen localities were studied in the Amazon, six, in the Andes, and eight, in the Pacific (Fig. 1, Table S1). These fields were orchards with an area of 0.1 to 12.7 ha; most of them (93.8%) with less than 3.4 ha (Table S2) and under traditional management practices in home gardens [30]. The fresh fruit is part of the rural diet in Colombia, and its sales represent

the main income of the producers during the harvest period (Graefe et al., 2013). The palm stands were mixed mainly with different types of Musaceae, cacao, and coffee, though coffee was used exclusively in the Andes (Table S2). The study locations were immersed in different topographic and climatic conditions. The Pacific region is a mixture of small mountains and flatlands, the Amazon region is topographically similar to the Pacific but slopes are steeper, given its location on the eastern side of the Andes; and the Andes region is mainly mountainous (Table S3). In relation to climate, the Amazon and Pacific show high levels of precipitation and temperature throughout the year; in contrast, the Andes region is highly variable and a marked decrease in temperature is observed with increasing altitude (Table S3).

Study species

Bactris gasipaes Kunth

The peach palm (*B. gasipaes*) has been domesticated by native Americans for centuries (Mora-Urpí et al. 1997; Clement et al. 2010). It is characterized by multiple, straight, cylindrical, unbranched stems of 6–24 m height, and a canopy of 10–30 pinnate leaves (Mora-Urpí et al. 1997). Peach palms can develop in wide ecological conditions, as it is documented by their distribution in the neotropics, from Nicaragua to Bolivia. Optimal development takes place at middle altitudes (< 800 m.a.s.l.), with relatively deep, fertile, well-drained soils, and continuous rain (2000–5000 mm/year) (Mora-Urpí et al. 1997). Peach palms can be cultivated as a monoculture or in an agroforestry systems; in the latter case, it is associated with different crops, such as cassava, cacao, and coffee (Graefe et al. 2013). There are more than 41 species of arthropods that have negative impacts on this crop (Couturier et al. 1996; Vásquez et al. 2000; Arroyo Oquendo et al. 2004; Pardo Locarno et al. 2016); incidence reports in Costa Rica and the Amazon are associated with large-scale cultivation (Mora-Urpí et al. 1997). The more serious infestations have been reported for the fruit borer *Palmelampus heinrichi* O'Brien & Kovarik 2000 (Sanabria Ujieta 2014), and the weevils *D. borassi*-*R. palmarum* (Pardo-Locarno et al. 2016; Gaviria et al. 2021).

Dynamis borassi and *Rhynchophorus palmarum*

The weevils *D. borassi* and *R. palmarum* are associated with palms (Löhr et al. 2015; Vásquez-Ordóñez et al. 2020), and they differ in morphology (Vásquez-Ordóñez et al. 2020) and biology. *Dynamis borassi* is reported in cultivated and native palms, though economic damage has been only reported in peach palms in Colombia (Couturier et al. 2000; Bautista Giraldo et al. 2020; Vásquez-Ordóñez et al. 2020; Gaviria et al. 2021). In the past, *R. palmarum* was the most important pest in american cultivated palm species, such as coconut, oil palm, and ornamental palms (Oehlschlager et al. 2002; Milosavljević et al. 2020). The interaction of each weevil species with peach palms is different: *D. borassi* lays its eggs in the inflorescences (Bautista-Giraldo et al. 2020; Vásquez-Ordóñez et al. 2020; Gaviria et al. 2021), while *R. palmarum* oviposits at the apex of the stem and into lesions in other plant parts (Alpizar et al. 2002). Both species are endemic to the Neotropical region, though the distribution of *R. palmarum*, which occurs from the United States of America to Argentina (Giblin-Davis 2001; Milosavljević et al. 2020), is greater than that of *D. borassi*. The temporal abundances of *D. borassi* are affected negatively by precipitation (Gaviria et al. 2021) and the weevil association with its host *Oenocarpus bataua* is stronger in disturbed forests (Bautista-Giraldo et al. 2020). *Rhynchophorus palmarum* is more active during rainy periods (Murguía-Gonzalez et al. 2017).

Sampling and response variable

At each of the 32 peach palm fields, we followed the variable area transect system for sampling (Sheil et al. 2002; Gaviria et al. 2021). In our case, a central line of maximum 80 m length and varying width was demarcated, according to the field size. Up to eight perpendicular rectangles, each with a width of 20 m and a length determined by the distance from the central line to the sixth palm showing signs of weevil damage, were located on both the right and left sides of the central line. The maximum length of the rectangles was 50 m for the cases where six damaged palms. The number of healthy and damaged palms were recorded, from which the proportion of infested palms was estimated.

Explanatory variables

Local variables

Eighteen local variables were recorded in all fields (Table S4). The first nine corresponded to semi-structured questionnaires (Table S5), which were focused on characteristics of the crop (e.g., age, variety, size) and management (e.g., insecticide, liming, and fertilizers use). Other seven variables were derived from georeferencing the boundaries of each crop with GPSMAP 64s Garmin. The points were loaded in ArcGis 10.5, where we estimated the area of each palm orchard with the “Calculate Geometry” function. In the same software, we used the SRTM 90-m DEM Digital Elevation Database (Reuter et al. 2007), and the “Slope” and “Zonal Statistics” functions to estimate the minimal, maximum, mean, deviation, sum, and range of slopes of the polygon. Two additional variables were calculated by evaluating vegetation within the transect (herein called other crops) in the same transect described previously. First, up to ten plants were recorded per species to estimate their density; second, the number of species (richness) of other crops different from peach palm and the Shannon Diversity Index were calculated with the “diversity” package in R (R Core Team 2023).

Landscape variables

Sixty-four landscape variables were determined for all fields (Table S6) following five consecutive steps for each crop. First, the geographic centroid coordinates were calculated using the “Calculate Geometry” function of ArcGis 10.5. Second, for each centroid coordinate, the most recent cloudless satellite image was searched. The images were taken by Sentinel-2 MSI: MultiSpectral Instrument, Level-1C (Baillarin et al. 2012) according to a search with Google Earth Engine (Gorelick et al. 2017). They were composed by the bands B2, B3, B4, B5, B6, B7, B8, B11, and B12. Third, the images were cut in a 1 km diameter circle and in each circle, three types of cover were identified: areas without forest (herein called non-forest), forest-peach palm crops (herein called forest), and water. Fourth, in each cover, at least 30 training points were arranged for executing a Random Forest – Supervised classification machine learning algorithm with 50 trees, in Google Earth Engine (Fig. S1). Fifth, with the classification, seventy-one landscape statistics were developed using the LecoS-QGIS plugin (Jung 2013), seven parameters were removed from the analysis given that they had no variability (Table S6).

Soil and climate variables

Sixteen soil types (Table S7) and eleven climatic variables (Table S3) were extracted from each geographic centroid coordinate of the peach palm fields. For the soils, the Soil Grids 250 m database for a depth of 0–30 cm (Hengl et al. 2017) was used, including the chemical and physical properties, as well as the soil type. For the climate variables, the original information were daily minimum and maximum temperature, and daily precipitation for 2010–2016, from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk et al. 2015) and Climate Data Record Based on Infrared Temperatures and Stations by the Climate Hazard (CHIARTS; Funk et al. 2019). For temperature variables, monthly averages were calculated and for precipitation, the monthly sums were estimated. With this information, eleven bioclimatic variables were determined (O'Donnell & Ignizio 2012), corresponding to the Annual Mean Diurnal Range (BIO 2), Isothermality (BIO 3), Maximum Temperature of Warmest Month (BIO 5), Minimum Temperature of Coldest Month (BIO 6), Annual Temperature Range (BIO 7), Annual Precipitation (BIO 12), Precipitation of Wettest Month (BIO 13), Precipitation of Driest Month (BIO 14), Precipitation Seasonality (BIO 15), Precipitation of Wettest Quarter (BIO 16), and Precipitation of Driest Quarter (BIO 17).

Data analysis

We followed two steps to synthesize the information. First, we evaluated the peach palm crop infestation levels at the three Colombian natural regions (Amazon, Andes, and Pacific) using a generalized linear model (GLM) with a binomial error distribution, and a posterior change to a quasibinomial distribution, according to overdispersion. Additionally, we performed a Principal Component Analysis (PCA) on the eighty-one quantitative variables measured at each crop that included local, landscape, soil, and climate variables; two variables were excluded due to the absence of information in some localities (i.e., crop age and palm spacing).

To examine the association of explanatory variables with peach palm infestations, we run a series of analyses. Local, landscape, soils, and climatic variables were analyzed separately, with the proportion of damaged palms as the response variable. At the local level, given the high number of explanatory variables, we first identified intercorrelations running Spearman tests in a correlation matrix for quantitative variables (Table S8) and associations using Fisher tests (Table S9) for qualitative variables. Once intercorrelated variables were identified, these were grouped for the following analytical step. The variables of the age of weevil infestation, harvest strategy, lime management, weed control, and crop distance were eliminated from these analyses due to missing

data (Table S4). In a similar way, two localities from the Amazon (corresponding to localities with the identification code ID 21 from Florencia-Caqueta and ID 27 from San Miguel-Putumayo) were deleted for analysis due to missing data (Table S4). Next, we took only one variable per 'intercorrelation' group and used it as an explanatory variable in combination with the rest of variables, keeping infestation as the response in a GLM. We iterated this process with each variable of the intercorrelation group and then moved to the next intercorrelation group to repeat the process until all possible GLM models were obtained. The GLMs error distribution was binomial and changed to quasibinomial due to overdispersion. The best model presented the lowest value of residual deviance.

In relation to landscape, soils, and climate variables, we used Partial Least Squares Generalized Linear Regressions (PLS-GLM; Bastien et al. 2005), with a "Binomial" family distribution for the response variable. We used the Akaike Information Criterion (AIC) to select the best model, and we compared the coefficient of determination (R^2). Subsequently, we calculated the coefficients of each explanatory variable and a 95% confidence interval (1000 bootstraps). Those landscape, soil, and climate variables showing confidence intervals different from zero in the PLS-GLM were then examined in a correlation matrix using the Spearman test to identify intercorrelated variables.

Finally, all the variables within each intercorrelated group were entered once at a time in combination with the rest of the landscape, soil, and climate variables in a comprehensive GLM, using infestation as the response. The error distribution of the GLM was binomial and changed to quasibinomial due to overdispersion. The best model presented the lowest value of residual deviance. We excluded the local variable weevil's trapping because it had been documented as presence and absence in this study. This condition does not allow explaining its relationship with level of infestation, because it has been shown for *R. palmarum*, that insect collection is affected by the trap design (Aldana-De La Torre et al. 2020; Mora-Castañeda et al. 2022) and kairomone proportion (Moya-Murillo et al. 2015) in Colombia. Additionally, it has been suggested that environmental conditions among different localities may affect capture efficiency and pheromone emission in traps for *R. ferrugineus* (Vacas et al. 2016), a species related to *D. borassi* and *R. palmarum*. Afterwards, we determined the differences among palm weevil infestation levels at the three natural regions for the significant variables identified in the comprehensive GLM.

All statistical analyses were performed in the software R version 3.6.2 (R Core Team 2023), with a significance level of 5% and the packages of "boot", "car", "multcomp", "lsmeans", "plsRglm", and "psych".

Results

Peach palm infestation levels and environmental conditions of the three Colombian natural regions

Peach palm infestations by *D. borassi* and *R. palmarum* were different among natural regions ($\chi^2 = 6.28$, $df = 2$, $P = 0.04$), with higher values for the Pacific, in comparison with the Amazon and the Andes ($z = 14.51$, $df = \text{inf.}$, $P < 0.001$; $\chi^2 = 7.61$, $df = \text{inf.}$, $P < 0.001$; respectively), and less differentiation between Amazon and Andes ($z = 5.31$, $df = \text{inf.}$, $P < 0.001$; Fig. 2a). Infestation ranged from 0.00 to 1.00 and the highest mean value was 0.25, at the Pacific. Environmental characteristics of the sites where peach palm crops were located were associated with each of the three natural regions (Fig. 2c, Fig. S2), with 44.7% of the variation explained for the first two components. PCA Axis 1 separated the three natural regions and was highly correlated to land cover and largest patch area of non-forest; and PCA Axis 2 separated the Andes region from the other two regions and was highly correlated to peach palm crop slope.

Local variables

Local variables were not related to the proportion of infested palms in the 27 evaluated crops according to the best of the 959 evaluated models (Table S10 and Fig. S3 and S4). The variable "weevil trapping" was associated with infestation proportion ($\chi^2 = 5.52$, $df = 1$, $P = 0.02$; Table S10) when the variable "crop age" was removed. Removing "crop age" left twenty-nine crops and 481 models. The "weevil trapping" variable was related to the natural region (Fisher Test $P < 0.001$, Table S11, and Fig. S4). On the other hand, the variable "Shannon diversity index of other crops" showed a negative relationship with infestation (Fig. 2b). Nonetheless, there was no difference in infestation between both types (i.e., without other crops and with more than one crop) of cultivation strategies ($\chi^2 = 0.95$, $df = 1$, $P = 0.33$).

Individual and combined analysis of landscape, soil, and climatic variables

Landscape variables explained more variation in palm weevil infestation than soil and climatic factors ($R^2 = 77\%$, 16% , and 51% , respectively; Table S12) when each set of variables was analyzed individually. For the landscape, the best PLS-GLM model included four components (i.e., diversity indices and non-forest, forest, and water land covers) and 22 variables that represented landscape configuration and composition (Fig. 3, S5, and S6 and Table S13). Landscape diversity indices and all three land cover types were relevant for palm infestation. Most significantly, non-forest fragmentation (e.g., fractal dimension index) had a positive effect on weevil infestations, while for the forest, significant factors were related with area (e.g., land cover) (Fig. 3). The water cover was the most variable, with about half of the descriptors as relevant (Fig. 3), but the number of localities including water was only 14 (Table S6). For soil and climatic variables, the best models had two (i.e., chemistry and physical characteristics) and one (i.e., temperature) component, respectively, with three variables being important within each component (Figs. 4 and 5, respectively; Fig. S7, S8, S9, and S10, and Tables S14 and S15). In the soil, the most important variables corresponded to carbon density, clay content, and coarse fragments, and, in the climate dataset, the most important variables corresponded to the diurnal and annual ranges of temperature and to isothermality. Isothermality “quantifies how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations” (O’Donnell & Ignizio 2012).

In total, eighteen variables contributed to palm infestations, according to the individual PLS-GLMs, after variables with missing data were removed. The correlation among these variables demonstrated a relationship between climatic and landscape variables, except with landscape fractal dimension of the non-forest and soil variables (Table S16). The landscape variables corresponding to number and fractal dimension of non-forest patches were positively related with the infested peach palm proportion according to the best model of the 4031 evaluated ($\chi^2 = 4.79$, $df = 1$, $P = 0.03$, $\chi^2 = 7.14$, $df = 1$, $P < 0.001$, Table 1, Fig. 6). Both variables were not associated with the variable of the natural region of crops ($\chi^2 = 3.91$, $df = 2$, $P = 0.14$, and $\chi^2 = 2.64$, $df = 2$, $P = 0.27$, respectively; Table S11).

Table 1

Statistics of the best generalized linear model within 4031 models for significant variables identified by the PLS-GLM to explain infestation by the palm weevils *Dynamis borassi-Rhynchophorus palmarum* in Colombian peach palm crops. Bold values correspond to the p-value < 0.05. The degree of freedom was one and the error distribution family was quasibinomial. The statistical tests of significant variables are presented in Table S10 and Figs. 3, 4, and 5.

Statistic result	Variable							
	Landscape				Soil		Climate	
	Total land cover	Shannon's Diversity index	Number of non-forest patches	Fractal Dimension index of non-forest	Organic carbon density	Organic carbon stock	Coarse Fragments	Isothermality
Chi square value for variable	0.523	2.986	4.785	7.135	1.649	0.379	1.856	0.208
Degree of freedom	1	1	1	1	1	1	1	1
P-value	0.469	0.084	0.029	0.008	0.199	0.538	0.173	0.648

Discussion

We evaluated the combined effects of agricultural management, landscape, topography, soil, and climate variables on infestation levels of peach palms caused by *D. borassi* and *R. palmarum* in Colombia. We found that landscape variables explain more variation in palm infestations than the other variables. The analytical approach that we used (i.e., Partial Least Squares-Generalized Linear Regressions, PLS-GLM) enabled the simultaneous examination of variables operating at multiple scales, minimizing decisions that would have added subjectivity during the analytical process.

The infestation levels of peach palm crops by *D. borassi* and *R. palmarum* were different among the Amazon, Pacific, and Andes natural regions in Colombia. This differentiation could be related to the history of pest occurrence in each region. The first records of damage were made in the Pacific in 2010; posteriorly, damage was reported in the Andes in 2017, and in the Amazon in 2018 (Gaviria et al. 2021). Given that infestation levels were variable within each natural region, it was important to examine the

relationship of variables at multiple scales and infestation levels independently of the natural region. Thus, our evaluation yielded variables that were significantly related to peach palm infestation but were not structured by the natural region.

Landscape metrics were the most important to explain palm infestation in our study. Specifically, the non-forest fractal dimension index and the number of non-forest patches were positively related to infestation. The fractal dimension index measures shape complexity and represents a common ecological process or anthropogenic influence affecting patches across a wide range of scales (Neel et al. 2004). In our study area, various forestal resources are used by local people leading to a type of disturbance whose main signatures are narrow trails and footpaths that subsequently turn into wider paths and eventually shape the edges of non-forest fragments. A similarly high fractal dimension has been described for cannabis-dominated patches (Wang et al. 2017); this crop demands management at a similar scale than that of the peach palm, in contrast to others such as timber extraction (i.e., which involves the use of machinery and vehicles). In the case of cannabis, the increase of fractal dimension per unit area was related to a conversion from large, contiguous forest patches to smaller, fragmented patches with more exposed edge and reduced core areas, similar to the processes that may be taking place at our sites. In relation to the number of patches, which indicates fragmentation of a land cover, this metric alone has been shown to be non-significant for some tropical pests (e.g., Lepidoptera, Syahidah et al. 2021), but its interpretation needs to be done in the context of each study case. In our study, the positive correlation between number of non-forest patches and infestation reinforces the hypothesis suggested by the fractal dimension index; that is, the contact or exposition between forest and non-forest is relevant for the weevil-palm interaction.

The relationship between peach palm infestation levels and the fractal dimension index and number of non-forest patches could be explained by the biology and ecology of *D. borassi* in a landscape context. First, this weevil is most likely the initiator of damage in peach palms (Gaviria et al. 2021). Second, *D. borassi* has been shown to be associated with the native palm host *Oenocarpus bataua* in secondary forests and in regeneration areas close to peach palm crops in the Colombian central pacific region (Bautista-Giraldo et al. 2020). Third, high abundances of the weevil (Gaviria et al. 2021) but low infestation levels were reported in localities of the Colombian central pacific region (Gaviria et al. 2021) where density of inflorescences of *O. bataua* were high [29]. We consider the observations made by Bautista-Giraldo et al. (2020) and Gaviria et al. (2021) in part of our study area, a representation of the ecological mechanism taking place in the three studied ecoregions (i.e., Pacific, Andes, and Amazon). That is, given that those forest sites with high densities of unopened inflorescence of *O. bataua* corresponded to high densities of *D. borassi*, but the lowest levels of peach palm crop infestation (Table S1), we conclude that *D. borassi* may switch from its natural host to peach palm crops in those localities where *O. bataua* is scarce. *Dynamis borassi*, though, may prefer its native host, *O. bataua*, over the peach palm. This preference is supported by evidences that show, first, that adding peach palm inflorescences to artificial diet in the laboratory did not have an effect on the developmental time of the weevil (Cuellar-Palacios et al. 2020), and second, that the weevil may be smaller when fed on the peach palm, in comparison to the native palm (Vásquez-Ordóñez et al. 2022). Additionally, *D. borassi* has a life cycle duration of six to seven months (Wattanapongsiri 1966; Cuellar-Palacios et al. 2020) and, while *O. bataua* has a continuous flowering phenology (Galeano and Bernal 2010), the peach palm is uni- and bimodal (Yangüez Bernal 1975). The presence of alternative hosts for the weevils would be key for reaching stable local populations. Another biological factor that would favor population stability is the capacity of weevils to move across the landscape. If it is assumed that *D. borassi* has a similar capacity to move as *Rhynchophorus* species (Hoddle et al. 2020, 2021), this movement would allow finding alternative hosts when peach palm inflorescences are not present, facilitating the survival of their descendants and the population.

The preference of the weevil for its native host may be interacting with processes at the landscape scale to shape spatial patterns of peach palm infestation. For instance, the differences in inflorescences *O. bataua* densities recorded in Bautista-Giraldo et al. (2020) for the central pacific region match the differences in number of non-forest patches recorded in our study for that region (Table S6). It is likely that the number of non-forest patches indicates a pattern of forest use by humans. *Oenocarpus bataua* is abundant in low altitude forests of the Pacific (Valencia Marin et al. 2008; Balslev et al. 2015) and it is used for various purposes, such as pulp, stem, and seed oil exploitation, and handcraft (Castaño-Arboleda et al. 2007; Valencia Marin et al. 2008; Ledezma-Renteria et al. 2014). In the central pacific region, as has been documented for other colombian regions, it is common that the palm is cut completely to harvest these products (A. A. Vásquez-Ordóñez, pers. comm.), and this practice has considerably reduced its abundance (Castaño-Arboleda et al. 2007). This mechanism is likely the reason why both non-forest fractal dimension index and number of non-forest patches are positively related to peach palm infestation, given that forest edge exposition is a requirement for the exploitation of the native palm.

Three scenarios result from the suggested ecological mechanism. First, a decrease of the native palm would push *D. borassi* to use other hosts, such as peach palm. In the second scenario, the presence of few larger and more regular non-forest patches (corresponding to regeneration areas) would represent more suitable habitats for *O. bataua* (Valencia Marin et al. 2008; Galeano & Bernal 2010; Bautista-Giraldo et al. 2020), with a consequent increase in abundance. This increase would make the weevil stay in the native palm inflorescences instead of switching to the peach palm. In a third scenario, related to the low infestations recorded in the Amazon and Andes, the landscape is dominated by few large and regular non-forest patches that, in these cases, corresponded to pastures (Vásquez-Ordóñez, unpublished results). Given that pastures are not suitable for alternative hosts of *D. borassi* (Bautista-Giraldo et al. 2020), this would leave peach palm as the only host. Based on our proposed mechanism it is likely that the *D. borassi* populations are reduced in the long term in peach palm crops as the exclusive host.

Previous studies have documented relevant landscape variables such as the number of non-forest patches and their shapes as associated with ecological processes related to edge effects and open sites (Farina 2008; Liu et al. 2008). These landscape variables may mediate the use of alternative hosts of the pest, as had been documented in insect-crop interactions (Ricci et al. 2009; Veres et al. 2013; Saeed et al. 2015). In our case, similar processes may be taking place, as *O. bataua* has been shown to be affected by the increase of forest edge (Browne and Karubian 2016) and human activity linked to opening sites (Aguilar 2005; Hernández Muñoz and Martínez Santacruz 2018).

Explanatory variables other than landscape, such as agricultural management, topography, soil, and climate were less correlated or not correlated to peach palm infestations. Part of this lack of correlations can be explained by biological aspects of the interacting species (i.e., weevils and palm) and by cultural practices. In relation to biology, *R. palmarum* has high vagility (Hoddle et al. 2020, 2021) which means that the effects of peach palm crop size, slope, and physical interference from other plants inside the crops may be negligible. In relation to management, it has been hypothesized that the harvest method may influence infestation by *R. palmarum*, especially when the stem is injured while climbing to the top, which would attract the weevil (Pardo Locarno et al. 2005). Our results do not support this hypothesis; it is likely that the palm has the capacity to generate slime in response to wounds (Weiner and Liese 1996), with no impact in the local infestation patterns. Second, at the moment of sampling many farmers used a specific pheromone to trap *R. palmarum*, but not *D. borassi* (Vásquez-Ordóñez et al. 2020; Gaviria et al. 2021). Additionally, we were not able to characterize via surveys the trap design and kairomone proportion used by each farmer in the traps (Moya-Murillo et al. 2015; Aldana-De La Torre et al. 2020; Mora-Castañeda et al. 2022). All these variables associated with the weevils' management interfere with our infestation estimations, and further studies should be conducted to understand these local effects. In relation to large-scale variables, Gutierrez et al. (2023) have tested the effects of precipitation, maximum temperature, and minimum temperature on the abundances of *D. borassi* and *R. palmarum* in the Colombian south Pacific and, similarly to our results, found no significant correlation.

A multi-scale approach enabled us to propose an ecological mechanism for palm infestation that has not been proposed before. Based on our results we hypothesize that global changes related to land use and invasion of exotic species will be relevant to palm crops in the tropics. The current environmental challenges that tropical agriculture in general and palm cultivation in particular face present an opportunity to use novel analytical techniques that enable the study of complex ecological processes.

Conclusions

In conclusion, landscape was more relevant than management, topography, soils, and climate to mediate the interaction between weevils and the peach palm in three natural regions in Colombia. We suggest that the combination of land use and a weevil's native host palm are part of an ecological mechanism that may be promoting peach palm infestation patterns at a landscape scale. In consequence, we recommend that palm management is designed with a landscape perspective; that is considering the conservation of alternative hosts for the weevils in the agroforestral plots. At the same time, it is necessary to evaluate new management strategies such as the use of the *D. borassi* pheromone, which is showing promising results (Gaviria et al. 2021). An interesting next step would be to examine how the drivers of global change examined here could be generating evolutionary changes in the interacting species.

Declarations

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Competing Interests

The authors declare that there are no conflict of interest.

Author Contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by Aymer Andrés Vásquez-Ordóñez. Analysis by Aymer Andrés Vásquez-Ordóñez, Wilmar Torres-López, and A. Carolina Monmany-Garzia. The first draft of the manuscript was written by Aymer Andrés Vásquez-Ordóñez and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available supplementary information.

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Figures

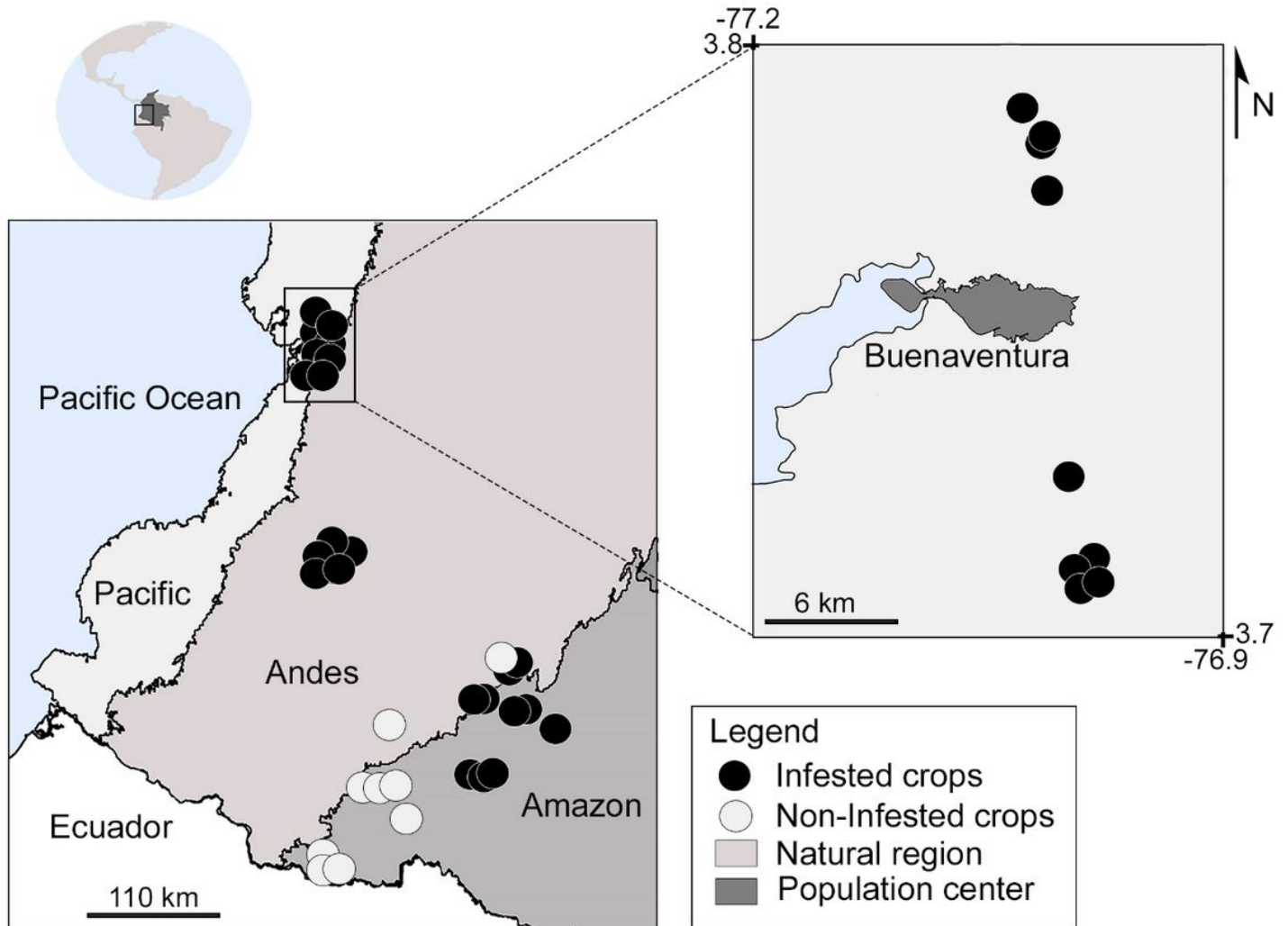


Figure 1

Geographical location of the 32 peach palm fields (circles) where infestation levels of *Dynamis borassi* and *Rhynchophorus palmarum* were studied in the Amazon, Andes, and Pacific regions in Colombia. The color of the circles represents the presence and absence of infestation in the peach palm (*Bactris gasipes*).

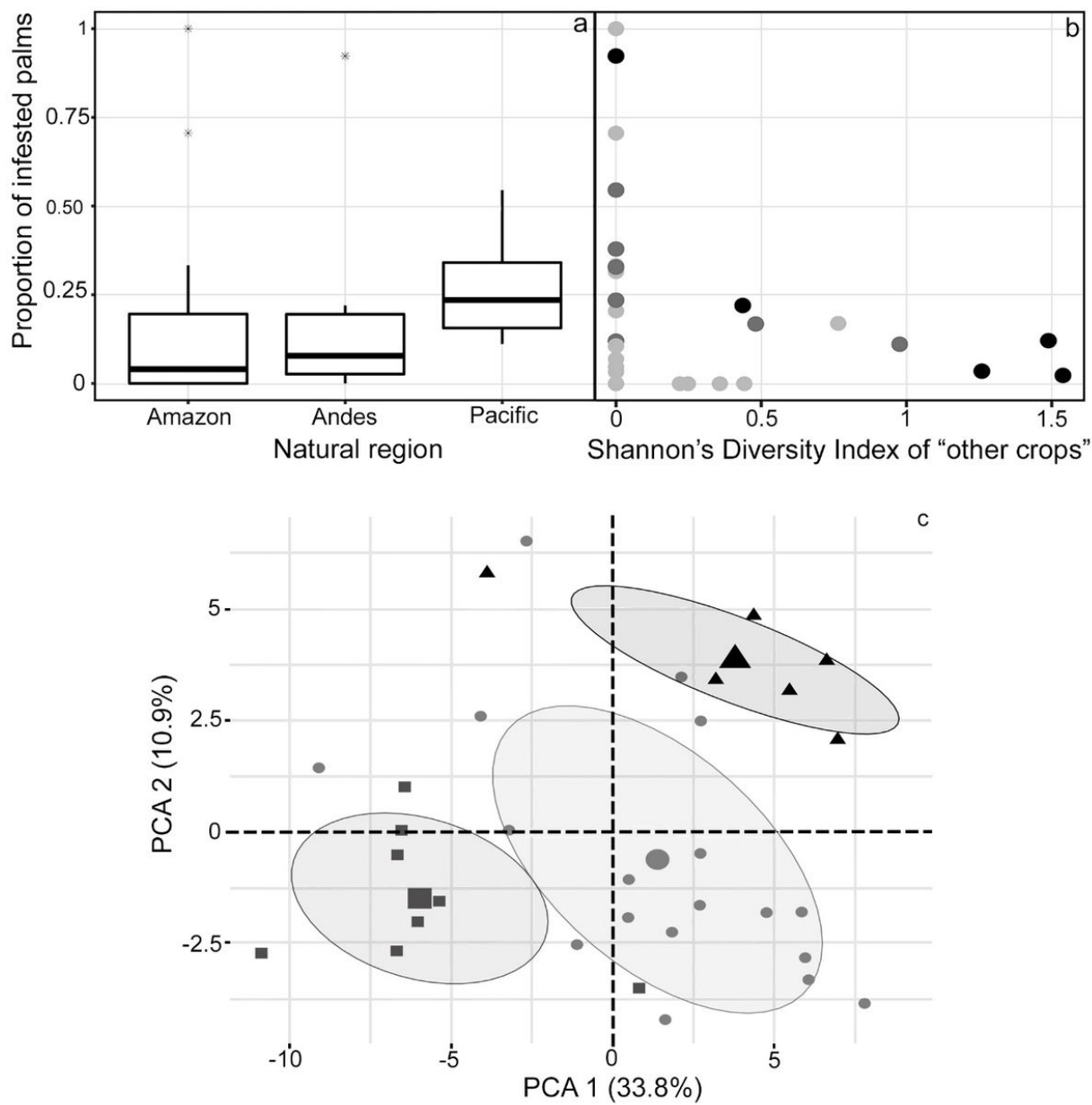


Figure 2

Proportion of infested Peach palms (*Bactris gasipaes*) by *Dynamis borassi* and *Rhynchophorus palmarum* in three Colombian natural regions (a) and Shannon Diversity Index of "other crops" or vegetation within the transect (b). (c) Each crop is plotted in relation to the first two principal components (PCA) of eighty-one quantitative environmental variables including local, landscape, soils, and climate variables. The light gray circles represent data from the Amazon, the black triangles represent data from the Andes, and the dark gray squares represent data from the Pacific. Ellipses represent data concentration in the principal component analysis.

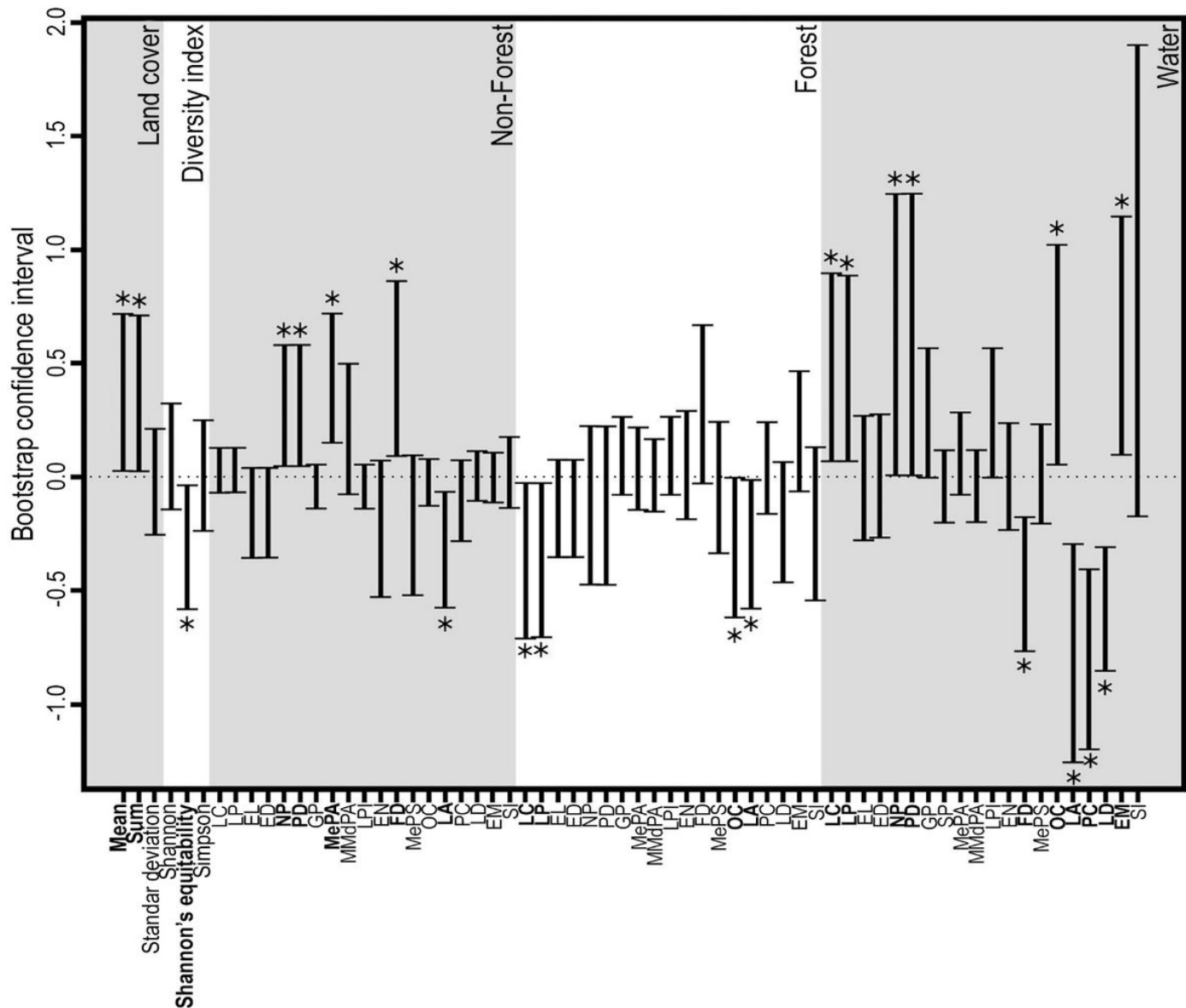


Figure 3

Bootstrap confidence intervals of landscape variables in the Partial Least Squares Regression for Generalized Linear Models (PLS-GLM) examining proportion of peach palms (*Bactris gasipaes*) infested by *Dynamis borassi* and *Rhynchophorus palmarum* in three natural regions in Colombia. LC: Land Cover, LP: Landscape proportion, EL: Edge length, ED: Edge density, NP: Number of patches, PD: Patch density, GP: Greatest patch area, SP: Smallest patch area, MePA: Mean patch area, MdPA: Median patch area, LP: Largest patch index, LPI: Largest patch index, EN: Euclidean Nearest-Neighbor distance, FD: Fractal dimension index, MePS: Mean patch shape ratio, OC: Overall core area, LA: Like adjacencies, PC: Patch cohesion index, LD: Landscape division, EM: Effective MeshSize, SI: Splitting index. The asterisks and variable names in bold correspond to intervals that differ from zero.

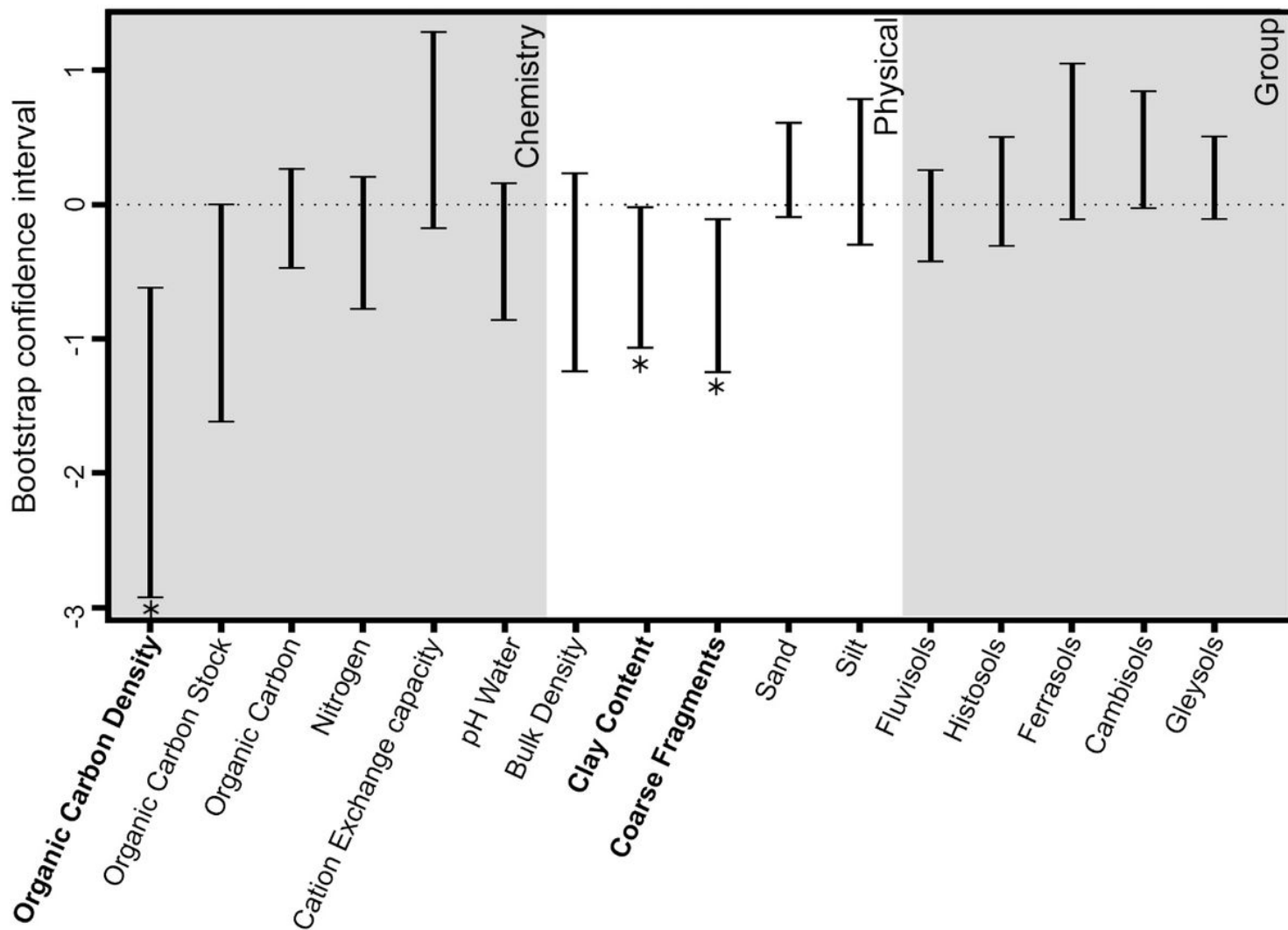


Figure 4

Bootstrap confidence intervals of soil variables in the PLS-GLM of the proportion of peach palms (*Bactris gasipaes*) infested by *Dynamis borassi* and *Rhynchophorus palmarum* in three natural regions in Colombia. The asterisks and variable names in bold correspond to intervals that differ from zero.

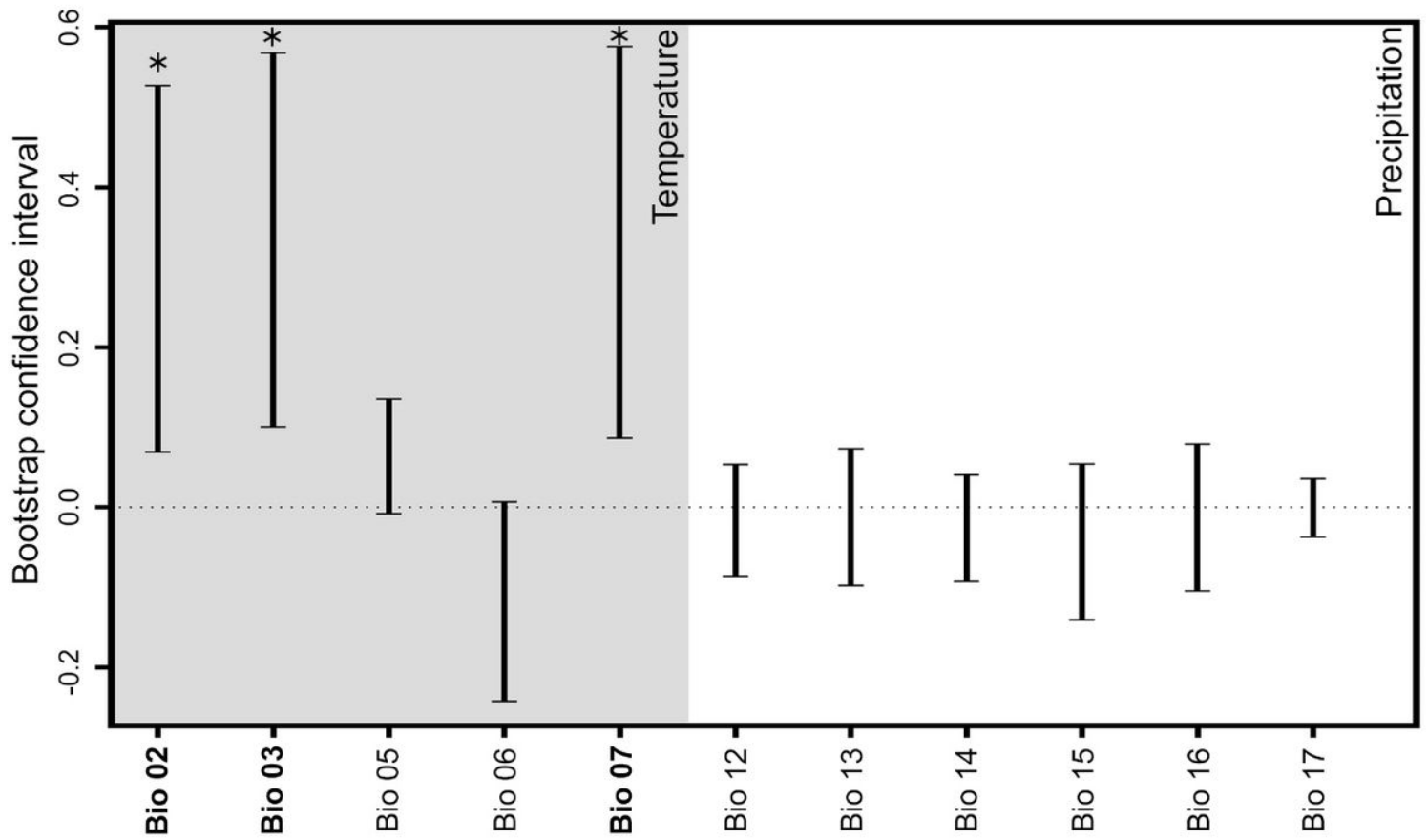


Figure 5

Bootstrap confidence intervals of climate variables in the PLS-GLM of the proportion of peach palms (*Bactris gasipaes*) infested by *Dynamis borassii* and *Rhynchophorus palmarum* in three natural regions in Colombia. Bio 02: Annual Mean Diurnal Range, Bio 03: Isothermality, Bio 05: Maximum Temperature of Warmest Month, Bio 06: Minimum Temperature of Coldest Month, Bio 07: Annual Temperature Range, Bio 12: Annual Precipitation, Bio 13: Precipitation of Wettest Month, Bio 14: Precipitation of Driest Month, Bio 15: Precipitation Seasonality, Bio 16: Precipitation of Wettest Quarter, Bio 17: Precipitation of the Driest Quarter. The asterisks and variable names in bold correspond to intervals that differ from zero.

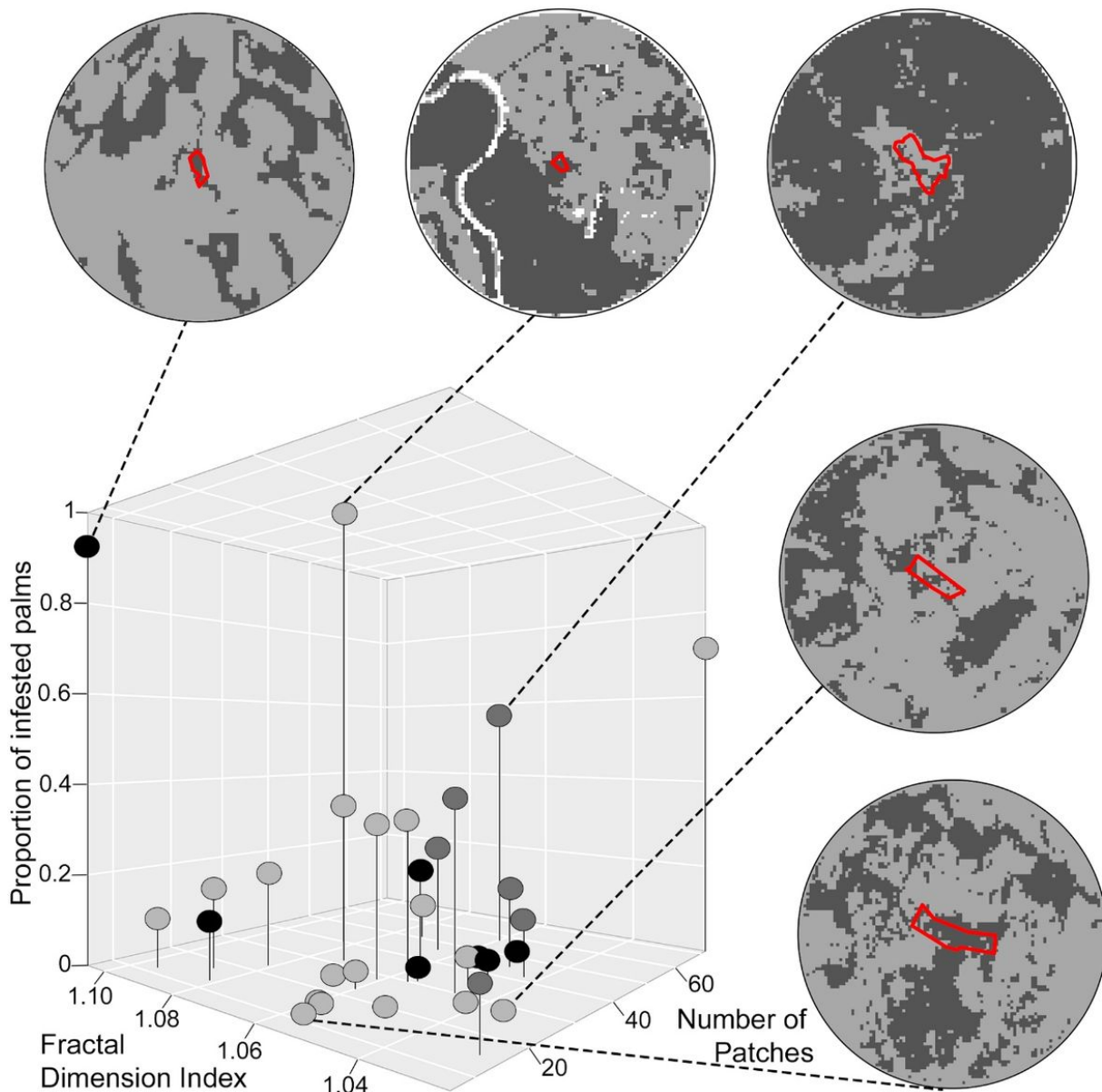


Figure 6

Proportion of peach palms (*Bactris gasipaes*) infested by *Dynamis borassi* and *Rhynchophorus palmarum* with respect to fractal dimension index and number of patches of non-forest cover. Light gray points represent the Amazon, black points represent the Andes and dark gray points represent the Pacific. Circular landscape buffers of one kilometer in diameter are illustrated around five crops as examples, where the dark gray pixels indicate forest, light gray pixels represent no forest, white pixels are water, and the red polygon shows the crop boundary.

Supplementary Files

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