



# 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 affects the economy of rural 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 peach palm is to design palm management with a landscape perspective that considers the conservation of alternative hosts for the weevils in agroforestral plots.

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## Introduction

Pest-plant communities are influenced by landscape composition and configuration (Kruess and Tscharncke 1994; Bianchi et al. 2006), topography, and climate (Davis et al. 1996) at large scales, according to evidence from temperate environments. Throughout the history of pest studies, 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 Tscharncke (1994) showed that high abundances of a pest were correlated to a high degree of isolation of the plot, which prevented natural enemies from maintaining viable populations there. Furthermore, including more than one scale at a time showed to be an efficient way to design integrated pest management strategies that were realistic (e.g., Begg et al. 2017).

Multi-scale approaches have been useful to study pest-plant interactions in the context of global change (e.g., Villa et al. 2020), which results from the influences of drivers operating at different scales, such as climate, land use, and invasive species, on ecosystems (Scherm et al. 2000; Sage 2020). While most of our understanding of pest-plant interactions at multiple scales have been built on evidence from temperate environments, fewer studies have tested the validity of those mechanisms in the tropics. Research in the tropics have shown a combined contribution of agricultural practices, landscape, and climate on infestation or pest abundance in cassava, coffee, lupine, maize, organic crops, papaya, 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 et al. 2019; Soti et al. 2019, Flores-Gutierrez et al. 2020, Struelens et al. 2021, Togni et al. 2021). For instance, by simultaneously examining land use and climate variables on the incidence of tropical organic farm pests', Togni et al. (2021) found that high precipitation, low temperature, and landscape fragmentation impacted positively on infestation. In another multi-scale example that included the effects of landscape and pesticide

use on papaya pests, Flores-Gutierrez et al. (2020) showed that pesticides negatively affected natural enemies and surrounding landscape affected pest abundances. While each of these examples may be translated into pest management practices for certain crops, an evident pattern is that the interactions among global change drivers are particularly complex in the tropics and results are crop-dependent. This limits generalizations that may be made about ecological mechanisms enhancing or suppressing pest outbreaks.

Ecoregional studies in tropical crops have shown to be important to assess complexity in pest dynamics (Savary and Willocquet 2020). Relationships among drivers at multiple scales may be understood especially when extensive crop areas are studied. For example, by examining differences in management, damage caused by pests, and weather among more than 400 rice farms covering a wide range of environments, Savary et al. (2000) found strong associations among the three variables at regional scales, and thus suggested that pest management strategies could be adapted throughout the region, rather than being site-specific. Similarly, when environmental and biological factors were correlated to crop pests at global scales, the ongoing dispersal of pests was found to be regionally constrained, emphasizing the importance of ecoregional studies to understand plant-pest dynamics (Bebber et al. 2014).

Another approach to understand pest outbreaks has been the examination of the interplay between native hosts, alternative hosts, and pests (e.g., Smith et al. 2001; Togni et al. 2021). At the field scale, a well-known agricultural practice has been to introduce plant host species to balance pests' infestations on targeted crops (e.g., Panizzi et al. 1997). Similarly, at landscape scales, crop-pest interactions have been shown to be mediated by the presence of alternative hosts in the surrounding natural habitats (Norris and Kogan 2000; Blitzer et al. 2012; Tscharncke et al. 2016; Kim 2017; Araujo et al. 2019). According to this evidence, alternative hosts may be used by pests when the crop is not available, promoting pest survival. At the same time, a different process may occur whereby an insect pest switches its host when a crop is introduced in a new region; the insect is closely associated to its native host, but the new resource can promote the insect movement toward the crop (Shapiro and Masuda 1980; Smith et al. 2001; Gavrilovic

et al. 2007). The study of this mechanism, though, involves historical data that is not easily available in tropical crops; in addition, globally this mechanism has been explored mostly through observational studies. Smith et al. (2001) found high rates of infestation in native *Gaylussacia* spp. by the blueberry maggot, *Rhagoletis mendax*, supporting the hypothesis that infestations observed in commercial fields may have originated from these infested native host plants. In a changing world we need to understand to what degree pest outbreaks are driven by species 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. The recent phytosanitary crisis in peach palms (*Bactris gasipaes*) in Colombia (Gaviria et al. 2021) is an opportunity to study an emerging pest in tropical ecosystems using a multi-scale approach. A limited number of multi-scale studies have been made to understand the interaction of weevils and cultivated palms, and this body of evidence suggests that including agricultural practices, landscape, and climate in multi-scale studies may be critical to explain pest-palm dynamics in some cases. 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).

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 (Kattan et al. 2004; Rangel-Ch 2015). Three ecoregions may be differentiated in the Colombian southwest (i.e. Pacific, Andes, Amazon), which result from geophysical effects on climate and biological communities. In addition, differences in historical records of palm damages and differences in agricultural practices at the scale of fields may be observed (e.g., use/not use of weevils’ attractants). 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 initial activity of *D. borassi* larvae (Pardo-Locarno et al. 2016; Vásquez-Ordóñez et al. 2020; Gaviria et al. 2021). The levels of infestation caused by these weevils are variable among and within ecoregions in the Colombian southwest (Gaviria et al. 2021), but the drivers shaping these spatial patterns of infestation 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 at a local scale (Bautista-Giraldo et al. 2020). Furthermore, in that region, the occurrence of *D. borassi* and *R. palmarum* were contrasting between two distant locations, with higher abundances at the northern site (Gaviria et al. 2021), where the availability of inflorescences of *O. bataua* were also higher (Bautista-Giraldo et al. 2020) and forest fragmentation was characterized by homogeneous forest patch shapes, in contrast to the southern sites. These lines of evidence suggest that *D. borassi* pest may have switched from *O. bataua* to peach palm and landscape may have been the driver of this process.

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* at 32 sites in the Colombian southwest to understand underlying ecological drivers of the current phytosanitary crisis.

## 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 of flora and fauna. All subjects gave their informed consent for inclusion in the study. The study was conducted in accordance with the Declaration of Helsinki.

## Study sites

The study was conducted in 32 peach palm production localities 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 1). 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 1) and under traditional management practices in home gardens (Graefe et al. 2013). The palm stands were mixed mainly with Musaceae, cacao, and coffee (exclusively in the Andes) (Table 1). 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 S1). The climate varies among regions: the Amazon and Pacific show high levels of precipitation and temperature throughout the year (annual precipitation: 2577.7–4150.7 and 3730.2–6162.0 mm; maximum temperature of warmest month: 27.4–30.5 and 33.2–33.5 °C; minimum temperature of coldest month: 15.4–22.0 and

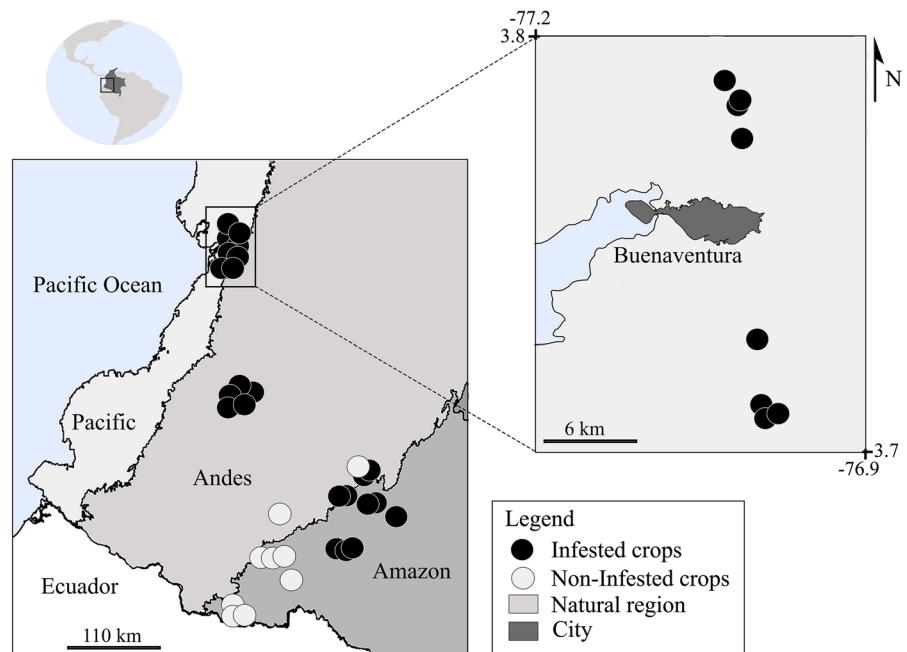
21.3–22.2 °C, respectively; Table S2); in contrast, the Andes region is highly variable and a marked decrease in temperature is observed with increasing altitude (annual precipitation: 2344–3002 mm; maximum temperature of warmest month: 23.9–26.8 °C, minimum temperature of coldest month: 14.2–17.5, Table S2).

## Study species

### *Bactris gasipaes*

The peach palm (*B. gasipaes*) is cultivated in the neotropical region, from Honduras to Bolivia (Mora-Urpí et al. 1997). This plant can be cultivated as a monoculture or in an agroforestry system; in the latter case, it is associated with different crops, such as cassava, cacao, and coffee (Graefe et al. 2013). It is used mainly for its fruit and heart of palm (Mora-Urpí et al. 1997; Graefe et al. 2013). The most important producers are: Brazil, Colombia, Peru, and Costa Rica (Clement et al. 2004). 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

**Fig. 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 gasipaes*)



**Table 1** Geographical coordinates, sampling dates of peach palm crops in Colombia, peach palm crop area, number of palms infested by *Dynamiis borassi* and *Rhynchophorus palmatum* (NIP), healthy palms (NHP), proportion of infested palms, and characterization of infested palms, and characterization of wild vegetation within the transect (herein called ‘other crops’)

Sampling type	ID	Natural region	Department	Municipality	Latitude	Longitude	Sampling date	Area (ha)	Number of perpendicular rectangles for sampling (Range of transect lengths in meters) <sup>a</sup>	NIP	NHP	IPP
Presampling	NA	Pacific	Nariño	San Andrés de Tumaco	1.5569	- 78.6972	Nov 30, 2017	NA	NA	NA	NA	NA
					1.5360	- 78.7023	Feb 14, 2019					
Sampling			Risaralda	Santa Cecilia	5.3408	- 76.1493	Feb 15, 2019					
			Valle del Cauca	Buenaventura	3.7084	- 76.9522	Jun 30, 2018					
	1		Valle del Cauca	Buenaventura	3.7629	- 76.9632	Jul 01, 2018	1.44	7 (37–50)	6	5	0.55 <sup>b</sup>
	2				3.9826	- 76.9804	Mar 31, 2018	1.15	8 (13–50)	45	92	0.33 <sup>b</sup>
	3				3.7015	- 76.9629	Jun 28, 2018	1.18	4 (50)	11	18	0.38 <sup>c</sup>
	4				4.0078	- 76.9916	Jun 7, 2018	1.44	8 (14.5–50)	40	130	0.24 <sup>b</sup>
	5				3.6905	- 76.9474	Jul 5, 2018	0.33	4 (50)	8	26	0.24 <sup>c</sup>
	6				3.6878	- 76.9591	Jun 28, 2018	1.03	8 (50)	4	32	0.11 <sup>c</sup>
	7				3.9894	- 76.9780	Jun 4, 2018	1.55	8 (50)	17	845	0.17 <sup>b</sup>
	8				3.9536	- 76.9764	Jun 01, 2018	12.65	8 (50)	17	125	0.12 <sup>b</sup>
	9	Andes	Cauca	El Tambo	2.3518	- 76.8937	Dec 01, 2018	0.35	6 (2–25)	36	3	0.92
	10				2.4097	- 76.8230	Nov 30, 2018	0.78	8 (50)	13	46	0.22
	11				2.4008	- 76.8487	Nov 29, 2018	1.63	5 (50)	12	87	0.12
	12				2.4027	- 76.8410	Nov 28, 2018	2.47	8 (50)	8	219	0.04
	13				2.4239	- 76.8418	Nov 30, 2018	0.78	5 (50)	3	126	0.02
	14			Santa Rosa	1.4243	- 76.4814	Feb 02, 2019	0.98	4 (50)	0	89	0.00
	15	Amazonas	Caquetá	Florencia	1.5015	- 75.6637	Feb 05, 2019	0.14	1 (10)	6	0	1.00
	16				1.3471	- 75.4752	Feb 05, 2019	0.81	2 (13–15)	12	5	0.71
	17				1.5514	- 75.8517	Feb 06, 2019	0.35	2 (45–50)	5	10	0.33
	18				1.5492	- 75.8608	Feb 06, 2019	0.16	1 (30)	6	13	0.32
	19		Putumayo	Puerto Guzmán	1.0230	- 75.9327	Feb 07, 2019	3.12	6 (30–50)	25	97	0.21
20		Caquetá	Curillo	1.0324	- 75.9985	Feb 07, 2019	0.56	2 (50)	9	44	0.17	
21			Florencia	1.4967	- 75.6535	Feb 05, 2019	0.97	4 (50)	14	118	0.11	

**Table 1** (continued)

Sampling type	ID	Natural region	Department	Municipality	Latitude	Longitude	Sampling date	Area (ha)	Number of perpendicular rectangles for sampling (Range of transect lengths in meters) <sup>a</sup>	NIP	NHP	IPP					
	22				1,7257	- 75,6558	Feb 08, 2019	0.34	2 (50)	4	80	0.05					
	23				1,7723	- 75,6514	Feb 04, 2019	0.11	1 (50)	2	27	0.07					
	24			Curillo	1,0381	- 76,0004	Feb 07, 2019	0.81	2 (50)	2	58	0.04					
	25			Florencia	1,7714	- 75,6575	Feb 08, 2019	0.50	2 (50)	0	79	0.00					
	26	Putumayo		Puerto Caicedo	0,6624	- 76,4704	Jan 30, 2019	2.56	7 (50)	0	335	0.00					
	27			San Miguel	0,3502	- 76,9676	Feb 01, 2019	8.06	7 (50)	0	162	0.00					
	28				0,3485	- 76,9269	Jan 31, 2019	1.77	8 (5)	0	483	0.00					
	29			Valle del Guamuez	0,4832	- 76,9738	Jan 31, 2019	0.91	5 (50)	0	277	0.00					
	30			Villagarzon	0,8889	- 76,6720	Jan 29, 2019	2.16	8 (5)	0	226	0.00					
	31				0,8842	- 76,5887	Jan 29, 2019	3.44	8 (50)	0	192	0.00					
	32				0,8881	- 76,6009	Feb 01, 2019	0.98	6 (50)	0	187	0.00					
<b>Other crops</b>																	
		<i>Alibertia patinoi</i>	Cassava	Citrus	Cocoa	Coffee	<i>Inga</i> sp.	Maize	Matisi-acordata	Mango	Musaceae	Pasture	Pineapple	Sugarcane	Colocasia-scutellenta	Trees <sup>d</sup>	Unknown
2	0	0	0	0	511	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	688	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	1556	0	0	0	0	0	0	0
6	40	0	0	0	270	0	0	0	0	412	0	0	0	1214	0	0	0
7	0	0	0	0	771	0	0	0	0	0	0	10	0	0	138	0	0
9	0	0	0	0	0	0	255	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	1865.74	0	0	0	0	0	0	0	0	350	0	0
11	0	0	0	0	857	333.33	15	0	0	20	667	0	0	333	0	0	1537.04
12	0	0	0	0	356	0	187	0	0	0	238	0	70	0	0	0	0
13	0	0	20	0	283	675.24	10	166.67	0	10	500	0	138.21	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	5000	0	0	0	0	0
18	0	0	0	0	500	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	1333	0	0	0	0	0	0	0

**Table 1** (continued)

ID	Other crops													Trees <sup>d</sup>	Unknown	
	<i>Alibertia patinoi</i>	Cassava	Citrus	Cocoa	Coffee	<i>Inga</i> sp.	Maize	Matis-acordata	Mango	Musaceae	Pasture	Pineapple	Sugarcane	Colocasia-esculenta	Trees <sup>d</sup>	Unknown
20	0	250	0	524	0	0	0	30	0	0	0	0	0	0	0	0
24	0	1666.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	95	0	0	0	0	0	0	65	0	0	0	0	0	3281.25
28	0	0	0	217	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	10	0	0	0	0	0	77	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	2352.99	0	0	0	0
31	0	0	0	995	0	0	112.5	0	0	30	0	0	0	0	0	0
32	0	0	10	0	0	0	0	0	0	825	0	0	40	0	0	0

<sup>a</sup>Each perpendicular rectangle had a width of 20 m and its length was determined by the distance from the central line to the sixth palm showing signs of weevil damage (Fig. 2). The maximum length of the rectangles was 50 m for the cases where six damaged palms were detected. See description in the “Sampling and response variable” section of the Materials and Methods. The exact date and number of healthy and infested palms of each perpendicular rectangle is reported in Table S3

<sup>b</sup>Peach palm crops coexisted with *Oenocarpus bataua*, which showed low abundances of unopened inflorescence, according to Bautista-Giraldo et al. (2020)

<sup>c</sup>Peach palm crops coexisted with *O. bataua*, which showed high abundances of unopened inflorescence, according to Bautista-Giraldo et al. (2020)

<sup>d</sup>These trees corresponded to wild and ornamental trees present within the peach palm crop examined

conditions. Optimal development takes place at middle altitudes (< 800 m.a.s.l.), with deep, fertile, well-drained soils, and continuous rain (2000–5000 mm/year) (Mora-Urpí et al. 1997). There are more than 41 species of arthropods that have negative impacts on this crop (Couturier et al. 1996; Vasquez 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* (Sanabria Ujieta 2014), and the weevils *D. borassi*-*R. palmarum* (Pardo-Locarno et al. 2016; Gaviria et al. 2021).

#### *Dynamis borassi* and *Rhynchophorus palmarum*

*Dynamis borassi* is a neotropical palm weevil reported from Panamá to Bolivia and Brazil (Wattanapongsiri 1966; Bautista-Giraldo et al. 2020; Gaviria et al. 2021). This weevil attacks eight palm species in plantations and forests (Wattanapongsiri 1966, Gerber et al. 1990; Couturier et al. 1998, 2000; Beserra et al. 2006; Bautista-Giraldo et al. 2020; Gaviria et al. 2021). The life cycle of *D. borassi* takes 150 days and the females have a mean oviposition capacity of 10 eggs over 50 days in laboratory conditions (Cuellar-Palacios et al. 2020). There are no reports on the dispersal capacity of

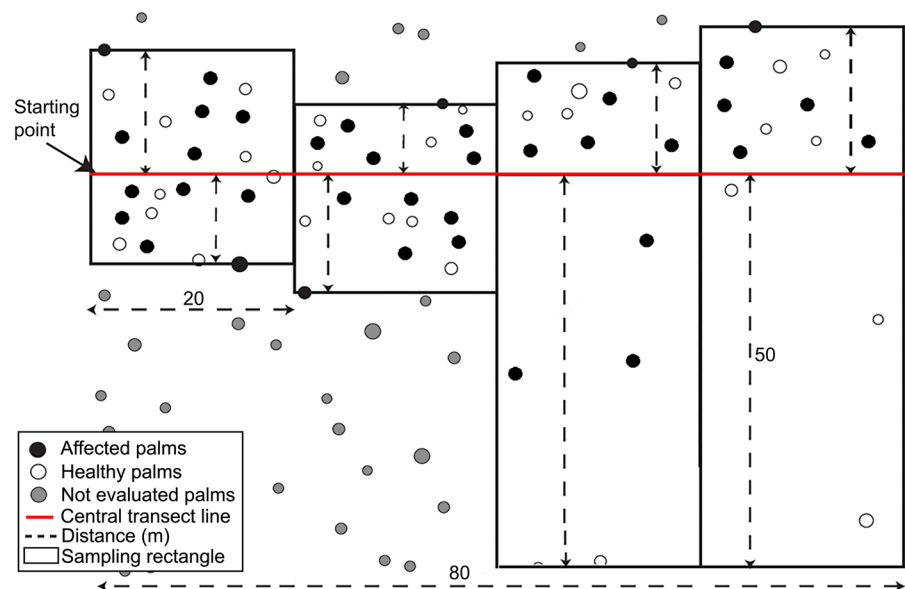
this insect pest. *Rhynchophorus palmarum* has been reported in all neotropical regions (Giblin-Davis 2001; Milosavljević et al. 2020) and it has recently invaded southern California (Milosavljevic et al. 2019). This weevil is associated with 10 Arecaceae host species (Milosavljevic et al. 2019) and is 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 life cycle of *R. palmarum* takes 79 days and the females have an oviposition capacity of 10 eggs per day in laboratory conditions (Hagley 1965). Adults have dispersal capacity of 150 km within a 24-h time frame, and they are able to detect host plants and breeding sites 1 km away (Hoddle et al. 2020, 2021).

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).

#### 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

**Fig. 2** Variable area transect method used for describing the peach palm infestation by the weevils *Dynamis borassi* and *Rhynchophorus palmarum* in 32 peach palm (*Bactris gasipaes*) crops in Colombia. The maximum length of the rectangles was determined by the distance from the central line to the sixth palm showing signs of weevil damage. Figure used with permission of authors of Gaviria et al. (2021) publication





demarcated, according to the field size (Fig. 2). 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 (Fig. 2). The maximum length of the perpendicular rectangles was 50 m in the cases where six damaged palms were detected (Fig. 2). The number of healthy and damaged palms were recorded in each perpendicular rectangles (Table S3) following the different damage stages reported by Gaviria et al. (2021), and the proportion of infested palms was calculated.

#### Explanatory variables

##### *Local variables*

Eighteen local variables were recorded (Table S1). The first nine were collected from semi-structured questionnaires (Table S4), which were focused on characteristics of the crop (e.g., age, variety, size) and management (e.g., insecticide, liming, and fertilizer 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 cultivated vegetation and wild and ornamental trees within the transect (herein called ‘other crops’) in the same variable area transect described previously. First, up to ten plants were recorded per species to estimate their density; second, the number of species (richness) of other cultivated vegetation and trees 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 S5) following five consecutive steps

for each peach palm 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 and peach palm (herein called non-forest), forest-peach palm crops (herein called forest), and water which correspond to rivers. Fourth, in each cover, at least 30 training points were arranged manually in each cover type in each 1 km diameter circle and a Random Forest—Supervised classification machine learning algorithm was executed (Breiman 2001; Gislason et al. 2006) with default parameter values and 50 as the number of “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 S5).

##### *Soil and climate variables*

Sixteen soil types (Table S6) and eleven climatic variables (Table S2) 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. The weighted mean (Quick and Chadwick 2011) was used for the three soil depths available in the database (i.e. 0–5, 5–15, and 15–30 cm). 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 (CHIRTS; 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 and Ignizio

2012), corresponding to the Annual Mean Diurnal Range, Isothermality, Maximum Temperature of Warmest Month, Minimum Temperature of Coldest Month, Annual Temperature Range, Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month, Precipitation Seasonality, Precipitation of Wettest Quarter, and Precipitation of Driest Quarter.

#### 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 distribution due to the nature of the response variable that corresponded to a proportion, and a posterior change to a quasibinomial distribution, to avoid overdispersion. Additionally, we performed a Principal Component Analysis (PCA) on the eighty-two 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).

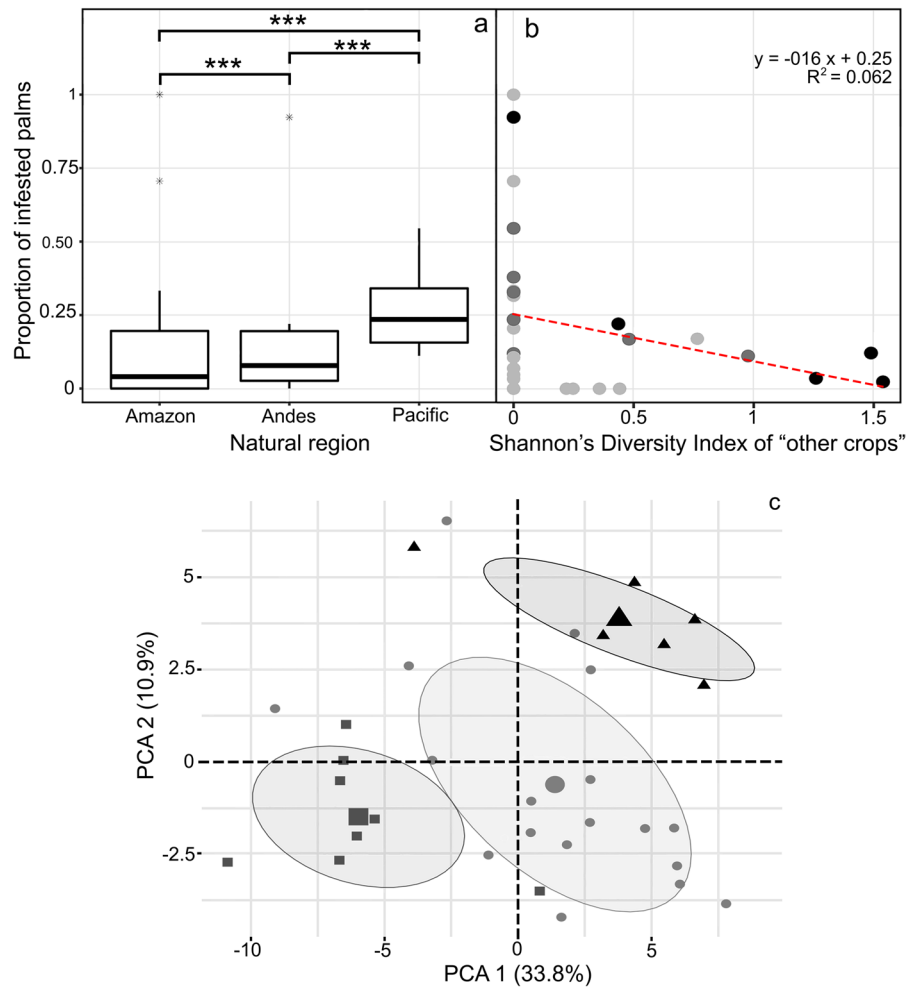
To examine the association of explanatory variables with peach palm infestations, we run a series of analyses. Local, landscape, soils, and climatic variables were analyzed separately, with the proportion of damaged palms as the response variable. At the local level, given the high number of explanatory variables, we first identified intercorrelations running Spearman tests in a correlation matrix for quantitative variables (Table S7) and associations using Fisher tests (Table S8) for qualitative variables (herein called “dependent variables”). 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 S1). 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 S1). Once dependent and informative variables were identified, these were grouped for the following analytical step (herein called “group of dependent variables”, see Fig. S2 to see the analysis step by step). Next, it was formulated

that all possible Generalized linear models (GLM) included: independent variables and one of the dependent variables from each group of dependent variables iteratively (Fig S2). This procedure was carried out to avoid collinearity or multicollinearity of the explanatory variables, guaranteeing independence between them while continuing to test all possible models. 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 (see Fig. S2 to see the analysis step by step), 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; de la 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. 2017), a species related to *D. borassi* and *R. palmarum*. In addition, we did not use the water landscape metrics because water was

**Fig. 3** Proportion of infested Peach palms (*Bac-tris 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). 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 (c). 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. \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$



present in only 14 of the 32 sites, which reduced the explanatory capacity of the model. Afterwards, we determined the differences among palm weevil infestation levels at the three natural regions for the significant variables identified in the comprehensive GLM.

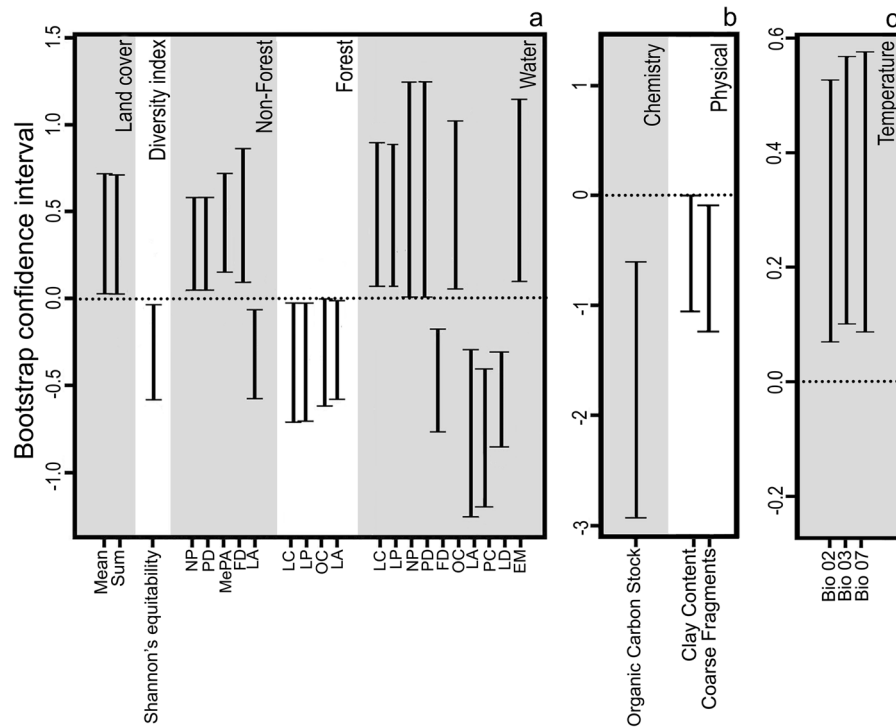
All statistical analyses were performed in the software R version 3.6.2 (R Core Team 2023), with a significance level of 5% and the packages of “boot”, “car”, “multcomp”, “lsmeans”, “plsRglm”, and “psych”.

**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 ( $z=14.51$ ,  $df=inf.$ ,  $P<0.001$ ;  $\chi^2=7.61$ ,  $df=inf.$ ,  $P<0.001$ ; respectively), and less differentiation between Amazon and Andes ( $z=5.31$ ,  $df=inf.$ ,  $P<0.001$ ; Fig. 3a). 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. 3c, Fig. S3, Tables S9, S10). The quantitative variables explained the 44.7% of the variation for the first two components (Fig. 3c, S4). PCA Axis 1 separated the three natural regions, which was mainly explained by the landscape variables (Table S9); and PCA Axis 2 separated the Andes region from the other two regions, which was mainly explained by the local and soil variables (Table S9).



**Fig. 4** Bootstrap confidence intervals of landscape (a), soil (b), and climate (c) variables with intervals that differ from zero 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 Colom-

bia. *NP* Number of patches, *PD* Patch density, *MePA* Mean patch area, *FD* Fractal dimension index, *LC* Land cover, *LP* Landscape proportion, *OC* Overall core area, *LA* Like adjacencies, *PC* Patch cohesion index, *LD* Landscape division, *EM* Effective MeshSize, *Bio 02* Annual Mean Diurnal Range, *Bio 03* Isothermality, *Bio 07* Annual Temperature Range

### 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 S11 and Fig. S5 and S6). The variable “weevil’s trapping” was associated with infestation proportion ( $\chi^2=5.52$ ,  $df=1$ ,  $P=0.02$ ; Table S11) 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 S12). On the other hand, the variable “Shannon diversity index of other crops” showed a negative relationship with infestation (Fig. 3b). 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

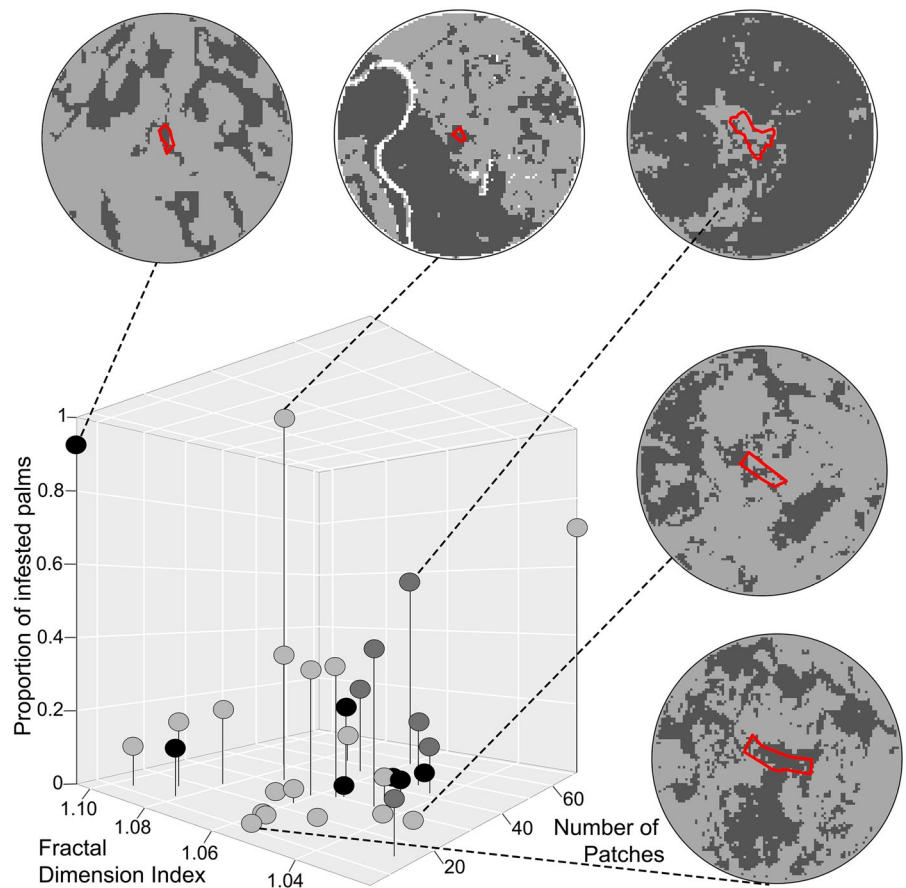
Landscape variables explained more variation in palm weevil infestation than soil and climatic factors ( $R^2=77\%$ ,  $16\%$ , and  $51\%$ , respectively; Table S13) when each set of variables was analyzed individually. For the landscape, the best PLS-GLM model included four components (i.e., diversity indices and non-forest, forest, and water land covers) and 22 variables that represented landscape configuration and composition (Fig. 4, S7, S8, and S9 and Table S14). 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. 4). The water cover was the most variable, with about half

**Table 2** 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

Statistic result	Variable							
	Landscape				Soil			Climate
	Total land cover	Shannon's Diversity index	Number of non-forest patches*	Fractal Dimension index of non-forest patches***	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

\* $p \leq 0.05$ , \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ . The degree of freedom was one and the error distribution family was quasibinomial. The statistical tests of significant variables are presented in Table S17 and Fig. 4

**Fig. 5** 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 non-forest, white pixels are water, and the red polygon shows the crop boundary



of the descriptors relevant (Fig. 4), but the number of localities including water was only 14 (Table S5). 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 (Fig. 4 Fig. S10, S11, S12, S13, S14, and S15, and Tables S15 and S16). 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 and 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 S17). 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 2; Fig. 5). 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 S12).

## 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 three ecoregions of Colombia. The analytical approach (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. We found that landscape variables explained more variation in palm infestations than the other variables.

Infestation levels were different between the Amazon, Pacific, and Andes natural regions of 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). In our study, though, no relationship was detected between infestation levels and years since the first detection of damage, as indicated by the farmers in the semi-structured surveys (Fig. S5,  $t=0.477$ ,  $df=12$ ,  $P=0.642$ ). However, due to missing data, we were not able to explore this variable in depth. In relation to other qualitative explanatory variables, the principal component analysis explained a low percentage of the observed variation among natural regions. 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 independent of the natural region.

## Impact of fractal landscape

Landscape factors 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 forest 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 to that of the peach palm, in contrast to others such as timber extraction. 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 edges 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 is case-specific. 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 between forest and non-forest land covers is relevant for the weevil-palm interaction.

Forest fragmentation measured as high non-forest fractality and high number of non-forest patches may be relevant to peach palm infestation through different ecological processes. First, *D. borassi* has a life cycle duration of six to seven months (Wattanapongsiri 1966; Cuellar-Palacios et al. 2020). At the same time, *O. bataua* has a continuous flowering phenology (Galeano and Bernal 2010), and the peach palm is uni- and bimodal (Yangüez Bernal 1975), which would restrict the use of peach palms by weevils in some periods of the year. But inflorescence densities of *O. bataua* have been observed to change biannually or greatly decrease (Collazos and Mejía 1988; Henderson 2002; Miller 2002; Rojas-Robles and Stiles 2009) and one valid question is to what degree this has been related to microenvironmental effects promoted by fragmentation, such as changes in light regimes and/or temperature that may influence on palms phenology. These phenological changes may force the weevil to search for other species, such as the peach palm. In the same line of thought, a possible effect of fragmentation on *D. borassi*'s predators may be relevant. There are no reports of predation on this weevil; but, in phylogenetically close groups such as species of the genus *Rhynchophorus*, natural enemies (i.e., parasitoid and predatory insects, birds, mammals, and entomopathogenic microorganisms) have been documented (Ortega-García et al. 2017). Given that a body of studies have evidenced multiple impacts of forest fragmentation and degradation on entomofauna, avifauna, mammals, and entomopathogenic fungi in tropical humid forests (Chaverri and Vilchez 2006; Perry et al. 2016; Durães et al. 2013; Cook et al. 2020), changes in species richness and/or abundance of potential predators of these weevils may take place under fragmentation (Durães et al. 2013). In our study, those sites showing high fragmentation, would correspond to sites with strong anthropogenic impacts, where weevil predators could

be more abundant and diverse, forcing these weevils to move to *B. gasipaes* crops, where predators' pressure is lower.

#### Host preference of the weevils

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 relation to its native host, in a landscape context. First, this weevil is most likely the initiator of damage in peach palms (Gaviria et al. 2021). Second, although *D. borassi* has been shown to be associated with different palm species throughout its distribution (Wattanapongsiri 1966, Gerber et al. 1990; Couturier et al. 1998, 2000; Beserra et al. 2006; Bautista-Giraldo et al. 2020; Gaviria et al. 2021), it has been exclusively associated with the native palm host *O. bataua* in secondary forests and in regeneration areas close to peach palm crops in the Colombian Central Pacific region (Collazos and Mejía 1988; 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 (Bautista-Giraldo et al. 2020). 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 1), 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* may prefer its native host, *O. bataua*, over the peach palm. This preference is supported by the following evidence. First, adding peach palm inflorescences to artificial diet in the laboratory did not have an effect on the number of larval instars, percent pupation, and developmental time of the weevil (Cuellar-Palacios et al. 2020), but the weevils were smaller when fed on the peach palm, in comparison to the native palm (Vásquez-Ordóñez et al. 2022). This suggests that under controlled conditions, the development and survival of *D. borassi*

larvae did not improve when fed on *B. gasipaes* inflorescences. Second, plant structures used by *D. borassi* for feeding and pupation have been documented on five occasions for five palm species. In the hosts *Astrocaryum carnosum*, *Cocos nucifera* and *O. bataua*, the weevil fed on the inflorescences and pupates inside the peduncular bract (Collazos and Mejia 1988; Gerber et al 1990; Peña Rojas and Jiménez 1994; Couturier et al. 1998; Bautista-Giraldo et al. 2020). In *B. gasipaes* and *O. mapora*, the weevil feeds on the inflorescences and stem of the palm tree and pupated within the stem (Couturier et al 2000; Gaviria et al. 2021). Based on literature, we compared the morphology of these palm species and found that the size of peduncular bract is greater in *A. carnosum* (100–170 cm length; Kahn and Millán 1992), *C. nucifera* (100 cm; Dransfield and Cooke 1999), and *O. bataua* (100–230 cm; Balick 1988) than in *B. gasipaes* (21–126 cm; Mora-Urpi et al. 1997) and *O. mapora* (50–86 cm; Balick 1988). This suggests that when inflorescences are not enough for *D. borassi* larvae to feed on, they move to the stem to continue the process. This plausible mechanism may explain the report of *D. borassi* larvae inside stems of *Euterpe oleraceae* (Beserra et al. 2006) and *Syagrus vagans* (Bondar 1940 and Landeiro (1941) cited by Wattanapongsiri 1966; Gerber et al 1990), which have a peduncular bract size that is similar to those of *B. gasipaes* and *O. mapora* (Bondar 1942; Henderson and Galeano 1996). Third, in the literature review we found that the confirmed attacks of *D. borassi* to palm trees were concentrated in the South American tropical region (Wattanapongsiri 1966, Gerber et al. 1990; Couturier et al. 1998, 2000; Beserra et al. 2006; Bautista-Giraldo et al. 2020; Gaviria et al. 2021). Most of these reports came from cultivated palms, except for three reports from wild palms (two of them endemic to Peru; Kahn and Millán 1992; Kahn et al. 2011). *Dynamis borassi* is distributed from Panama to southern Brazil (Wattanapongsiri 1966). Its geographic overlap with wild palm species throughout different ecoregions, and with cultivated palms in tropical South America suggests that the weevil is associated primarily with some native palm species in forests, as Bautista-Giraldo et al. (2020) have shown. The study of the association with *B. gasipaes* crops, the best studied to date, indicates that the current levels of damage and geographical extent are recent. Before the publication of Pardo-Locarno et al. (2016)

and Gaviria et al. (2021) there was only one report of this association for the Colombian Central Pacific region (Pardo Locarno et al. 2005), and no economic damage was observed. Fourth, 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 the population.

The preference of the weevil for its native host may be related to 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 S5). 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 scenarios of ecological mechanism section) 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 (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 were positively related to peach palm infestation, given that forest edge exposition would facilitate the access to and exploitation of the native palm.

#### Scenarios of ecological mechanism

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 palms. A landscape effect would interact with altitude, which is negatively correlated with densities of its native *O. bataua*, eventually impacting on *D. borassi*. In fact, the peach palm crops at each natural region in this study were located at



18–45 m.a.s.l. (Pacific), 226–1072 m.a.s.l. (Amazon), and 1000–1457 m.a.s.l. (Andes). While palm abundance has been documented to decrease with altitude in southern Amazonia and Costa Rica (Eiserhardt et al. 2011), this variable also affected palm species distribution in a wet lower montane forest in Ecuador, canopy palm community in a terra firme rain forest in the Amazonian Ecuador and Costa Rica, and palm richness in New Guinea (Eiserhardt et al. 2011). All host plants reported for *D. borassi* across its distribution were located at low altitudes, except for *O. bataua* (results not shown), which anyhow showed higher densities at low altitudes, according to our literature review. In the second scenario, the presence of few larger and more regular non-forest patches (corresponding to low-vegetation areas that may have remained after forest clearance) would represent more suitable habitats for *O. bataua*, 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 an exclusive resource.

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 2018) and human activity linked to opening sites (Aguilar 2005; Hernández Muñoz and Martínez Santacruz 2018). First, edge effects and open sites may impact on the survival of different stages of *O. bataua*. The number, morphological characteristics, and survival of the seedlings have been shown to be negatively correlated with shade (Rojas-Robles et al.

2008; Karubian et al. 2016). Considering that this plant can take from 12 to 40 years to grow from seedling to an adult (i.e., producing inflorescences (Guarín et al. 2014), complex dynamics would take place due to forest clearings at our sites. In smaller, irregularly-shaped clearings, it is likely that, although the seedlings had favorable conditions to grow, light hours were not enough on their way to adulthood. This would cause *D. borassi* to search for other hosts such as *B. gasipaes* crops, increasing its infestation levels. In the other scenario, a smaller number of patches that are more homogeneous in shape may affect the survival of the seedlings, but the few that survive can grow rapidly and manage to produce inflorescences, generating the opposite effect. Second, forest fragmentation may decrease the dispersion and genetic diversity of *O. bataua*. It has been suggested that a decrease in *O. bataua* dispersers explains the aggregate distribution of its seedlings (Sist and Puig 1987; Kahn and de Granville 1992; Rojas-Robles et al. 2008) and the differences in genetic diversity in forests with different levels of fragmentation (Browne et al. 2015; Browne and Karubian 2018). On the other hand, it was shown that this aggregate pattern of seedlings can increase mortality due to seed-boring insects and fungal attacks (Rojas-Robles et al. 2008) that may be related to edge effects. Third, the patterns of fragmentation at our sites may reflect a historical process of forest use, by which resources have been extracted for centuries, first with no apparent impact on forest connectivity but then promoting the opening of roads and small populations that may have extended edge areas and affected the dispersal and establishment of *O. bataua* plants, forcing the weevil *D. borassi* to attack nearby crops of *B. gasipaes*.

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 mobility (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; de la 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 conducted across three ecoregions 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 native host palm distribution are part of an ecological mechanism that promotes 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 agroforestry fields. 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.

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

## Declarations

**Conflict interest** The authors declare that there are no conflict of interest.

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