Sociobiology 68(2): e5928 (June, 2021) DOI: 10.13102/sociobiology.v68i2.5928

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Measuring the effect of long-term pitfall trapping on the prevalence of epigeal arthropods: A case study in the Pacific Coast of Colombia

José M Martinez[1], Rubilma Tarazona[1], Bernhard L Lohr[1], Consuelo A Narvaez[2]

1 - Corporación Colombiana de Investigación Agropecuaria – Agrosavia, Colombia
2 - Universidade Federal de Viçosa, Department of Entomology, Viçosa, MG, Brazil

Article History

Edited by
Eduardo Calixto, University of Florida, USA
Received 21 October 2020
Initial acceptance 29 December 2020
Final acceptance 24 April 2021
Publication date 11 June 2021

Keywords
Arthropods population, *Ectatomma ruidum*, long-term trapping, pitfall trapping.

Corresponding author
José M. Martinez
Corporación Colombiana de Investigación Agropecuaria – Agrosavia
Km 14 Vía Mosquera – Bogotá
Código Postal: 250047 - Colombia.
E-Mail: jose.martinez.rioja@gmail.com

Abstract

Pitfall trapping remains one of the most frequently used methods to assess ground-active arthropods' diversity and density. Yet, one of its main drawbacks, the possibility that repeated collecting may affect the study objects' population, has not been formally tested. We studied the effect of a yearlong epigeal pitfall trapping exercise with 22 fortnightly capture events in four differently disturbed areas at the Colombian Pacific coast. A transect of 100 m length with ten equidistant pitfall traps was established in each area, and the traps were operated twice a month for 24 hours. Using count data regression models, we find that trapping did not affect subsequent captures when we analyzed non-ant arthropods. For ants, regression estimates indicate that each subsequent trapping in highly-disturbed environments ended, on average, reducing all ants in between -3.8 and -4.1%, and *Ectatomma ruidum* between -4.7 and -5.1%. We recommend bio-ecological aspects of the species under study be considered when interpreting results. This is important for future studies that rely on this method to deliver consistent estimates of population sizes or study their dynamics through time. At the same time, it is also a call for scientists to revise more carefully how species' peculiar traits may limit the reliability of traditional methods.

Introduction

Pitfall trapping is one of the most frequently used methods to assess ground-active arthropods' diversity and density (Brown & Matthews, 2016; Greenslade 1964; Southwood, 1978). Its advantages and drawbacks have been the subject of discussion for a long time (Adis, 1979, Southwood & Henderson, 2016). Many attempts have been made to correct some of the most salient biases resulting from it (Greenslade, 1964; Hayes, 1970; Gist & Crossley, 1973; Luff, 1975). Sheikh et al. (2018) provide a detailed review on the use of pitfall trapping for ants worldwide. However, despite the many complaints about the method and the voluminous literature about the subject, the possibility that repeated epigeal collecting may affect the population size of the study objects (Southwood, 1978) is a claim that has never been adequately tested.

Greenslade (1973) and Joosse (1965) define a "digging-in effect" as the repeatedly found evidence of considerably larger captures right after pitfall traps have been installed when compared to the observed captures in subsequent catch counts. There are mainly four plausible causes for a systematically diminishing number of ant captures because of pitfall traps (Greenslade, 1973), namely: (a) penetration of nest galleries while setting up the traps; (b) traps are coincidentally located between nests and/or permanent food sources, i.e., traps over food trails; (c) ants exploring new features within their usual territories, and (d) depletion of populations. Joosse and

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

Kapteijn (1968) suggest an additional short-term digging-in effect, observed when epigeal traps are operated right after being installed. There is a systematic increase in the early captures of Collembola (Joosse & Kapteijn, 1968) and some ant species (Greenslade, 1973) since their locomotory activity also increases because of higher concentrations of CO_2. More recent studies have tested how the robustness of pitfall trapping is affected by habitat specificities (Jiménez-Carmona et al., 2019), the timing of pitfall opening after installation (Lasmar et al., 2017), and length of the sampling interval (Schimel et al., 2010). Still, the hypothesis of a decrease in observed captures resulting from the reduction of ant populations caused by the pitfall traps, as proposed by Jansen and Metz (1977), has never been formally tested.

We reanalyzed datasets generated by Löhr and Narváez (2021) during a year-long study in the Pacific lowlands of Colombia to identify surface-active predators that could be useful for controlling the oil palm root borer, *Sagalassa valida* Walker (Lepidoptera: Brachodidae), in four different environments. Some of the datasets seemed to indicate that different dynamics were present in the environments and the possibility of a diminishing number of arthropod captures over time, even though the sampling design was low-intensity. We test whether there is a long-term trapping effect on the subsequent captures of all groups of recorded arthropods through plot-fixed effects and plot-level count data regression models. These methods differ from most studies that try to model the dynamics of catches from pitfall trapping, which usually rely on ANOVA (or derivations of it) and/or log-linear regression analysis. We explain why count models that directly account for high-variance data better help capture the nature of the available information, hence better modeling the effect of pitfall trapping.

We argue why the experiment's structure helps correctly identifying a reduction of population effect, which is not confounded by other possible digging-in effects. Hence, it allows us to statistically determine the impact of long-term pitfall trapping over the prevalence of ground-active arthropods.

Materials and methods

The study area was within 564 ha of the El Mira Research Center (1° 32′ 58″ N, 78° 41′ 21″ W) of the Corporación Colombiana de Investigación Agropecuaria [Colombian Corporation for Agricultural Research] (AGROSAVIA), dedicated to research on oil palm (*Elaeis guineensis* Jacq.), peach palm (*Bactris gasipaes* Kunth), cacao (*Theobroma cacao* L.) and non-timber forestry products. The center is located 38 km southeast of Tumaco, in Nariño Department (Colombia), at 16 m. a. s. l. (Figure 1). The annual mean precipitation is 3,067 m.m., while the average temperature is 25.5ºC (Reyes, 2012). An on-site weather station recorded hourly solar radiation and daily rainfall data. Areawide flooding (i.e., more than 100 mm in the last 24 hrs.) occurred twice, and it was recorded to control for its possible effect on ground active arthropods.

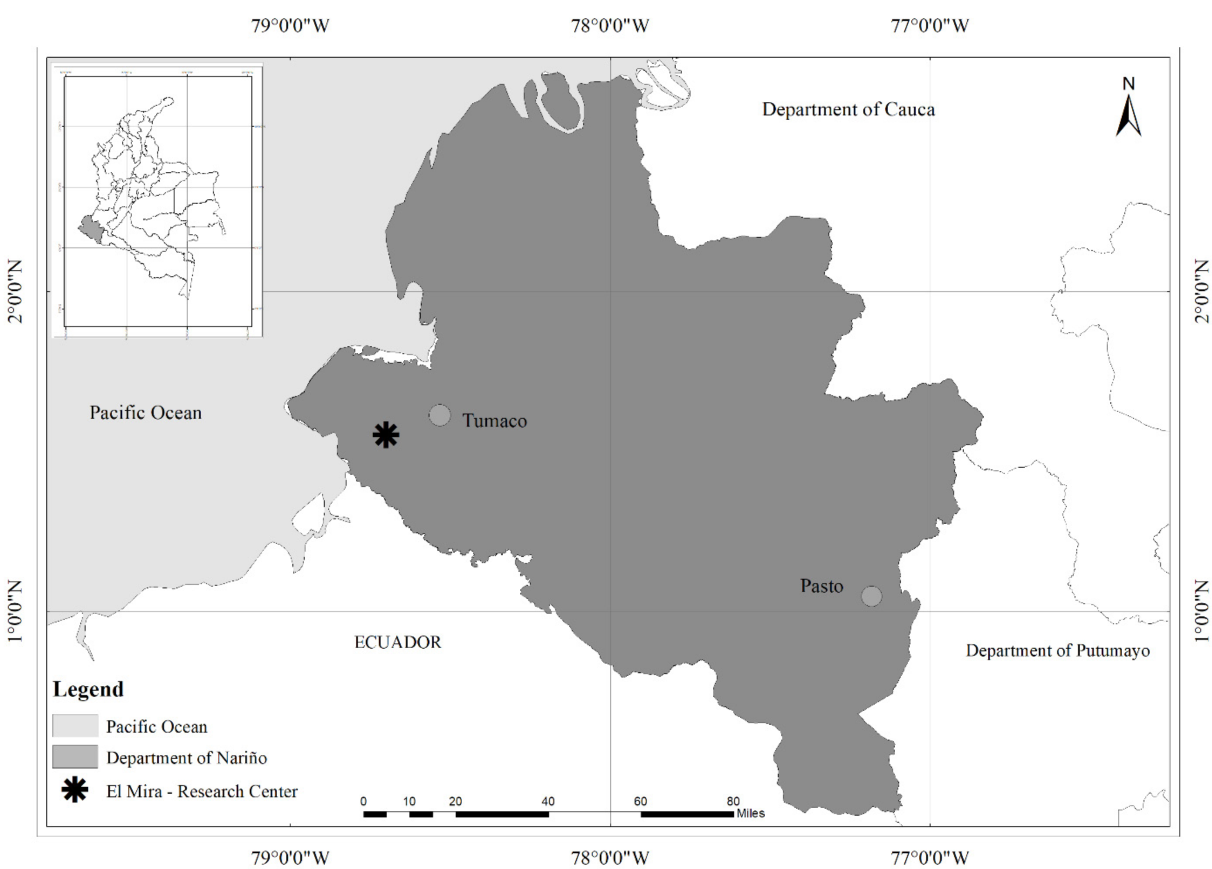

Fig 1. Geographic location of El Mira Research Center, Tumaco, Pacific Coast of Colombia.

The set-up of the study consisted of four transects, each a straight line of 100 m length with ten traps each at 10 m distance, located in plots with different levels of disturbance: a secondary forest regrowth with over ten years without interference (14 ha, transect parallel to and about 20 m from the forest edge); a 19 years old peach palm plantation (9.9 ha); a seven years old oil palm plantation (3 ha) and a three years old oil palm plantation of 14 ha. Routine management practices (fortnightly harvesting, quarterly weeding, and half-yearly fertilization) were implemented in the palm plantations while the secondary forest remained without interference. Traps consisted of 150 ml conical plastic cups (upper Ø 60 mm, 55 mm height), two of which were interred with the rim of the upper cup flush with the soil surface. For the collections, the upper cups were exchanged for cups filled with 50 ml water and a drop of dishwashing liquid. The time of each exposure was 24 hours. Between capture events, the upper cup was covered with a lid. Collections were made fortnightly with two exceptions in August 2016 and February 2017, when only one collection could be made. The collected material was processed in the laboratory, where all ants were removed and stored for posterior counting and identification. All other arthropods were counted individually and identified to order or family level where possible and grouped as follows: Hymenoptera, Diptera, Coleoptera, Hemiptera, Arachneae, Acari, Collembola, and others.

To check for the effect of temperature and sunshine hours, we calculated the average values of the period before the capture. We added them as a covariate to model capture events via Poisson and Negative Binomial Type 2 regression. To assess flooding impacts, we included an index variable that accounts for whether there was such an event immediately before the concurrent count. Before modeling the trends of captures across the four areas of interest, we test for statistical differences in captures between them for non-ant arthropods, ants, and *Ectatomma ruidum* via MANOVA (Stevens, 2002). This is an *F*-test where the null hypothesis states that the three response variables are the same across the four different plots.

We used count data regression models to model the effect of repeated trapping on the prevalence of arthropods across the plots (Cameron & Trivedi, 2005). We assumed that the observed counts of arthropods (Y) followed a Poisson distribution with the usual probability mass function

(1) $\Pr[Y = y] = \frac{e^{-\mu}\mu^{y}}{y!}$,

where μ is the scale parameter or the expected value of y. More specifically, we followed the standard exponential mean parametrization setting, where

(2) $\mu_i = \exp(x_i'\beta)$,

or, simply put, a generalized linear model with a Poisson error vector. For our study, the covariates set (x_i) included the round of trapping when the count was observed ($Round_{jt}$), and a binary variable indicating whether the capture event occurred right after a flooding event in the plots (CAF_t). We ran an overall regression including fixed effects for three of the plots (using the secondary forest as the base category) and four additional regressions to test for plot-specific effects. All regressions were performed for arthropods, all ant species, and *Ectatomma ruidum* only counts. Namely, at the overall level, we assumed that the rate parameter for trap i from plot j at the moment t was

(2') $\mu_{ijt} = \exp(\beta_0 + \beta_1 Round_t + \beta_2 CAF_t + \eta_j)$,

whereas for each plot would follow

(2'') $\mu_{it} = \exp(\beta_0 + \beta_1 Round_t + \beta_2 CAF_t)$.

Furthermore, for every regression, we also fitted a model including same-day total solar radiation (W/m^2) and precipitation (mm), since evidence suggests that these variables directly affect the behavior of ground arthropods, especially *Ectatomma ruidum* (Santamaría et al., 2009). The data is available from a hydrometeorological station installed in the research center, within 200 m from the plots, so we assume the precision to be high. Now, letting $SolRad_t$ and $Precip_t$ be the notation for solar radiation and precipitation, respectively. The additional overall model is

(3)
$\mu_{ijt} = \exp(\beta_0 + \beta_1 Round_t + \beta_2 CAF_t + \beta_3 Solrad_t + \beta_4 Precip_t + \eta_j)$,

whereas for each plot, it follows

(3')
$\mu_{it} = \exp(\beta_0 + \beta_1 Round_t + \beta_2 CAF_t + \beta_3 SolRad_t + \beta_4 Precip_t)$

Broadly, we were interested in testing the null hypothesis where the semi-elasticity $\beta_1 = 0$. This is, we tested whether repeated trapping influences the observed counts of arthropods, all ant species, or *E. ruidum*. Estimation of the parameters followed quasi-maximum likelihood (QML), and the standard errors were corrected for robustness due to the data's high variance (Cameron & Trivedi, 2005; Greene, 2012). Since bias due to data overdispersion might not be overcome solely by using robust standard errors, we further extended our analysis by including a negative binomial (NB2) regression approach, which yields unbiased estimators even in the presence of overdispersion. The NB2 strategy suggests that the observed counts would again follow a Poisson data generating process with scale parameter $\lambda = \mu\nu$, where ν is a positive, independently and identically distributed shock so that the expected value of y is still μ, the variance now follows[1]

(5) $V[y|\mu, \alpha] = \mu(1 + \alpha\mu)$

so that high-order variance is now reflected as a quadratic function of the mean.

Results

Nearly a third of all captures through all trapping rounds (33%) were of *Formicidae*, whereas Collembola captures accounted for 35% of the total (Fig 2). A complete list of the taxonomic groups, numbers collected, and land use influence is available in Löhr and Narváez (2021). The data distribution shows a strong positive asymmetry[2] for overall captures and somehow less overall variance for the captures of ants (Fig 3). Also, we noticed how the overall captures are related to the distribution of captures of arthropods that are not ants, particularly Collembola – i.e., the statistical distribution of overall captures is more similar to that of non-ants. These initial findings further reassure our modeling strategy's appropriateness, which relies on count-data non-

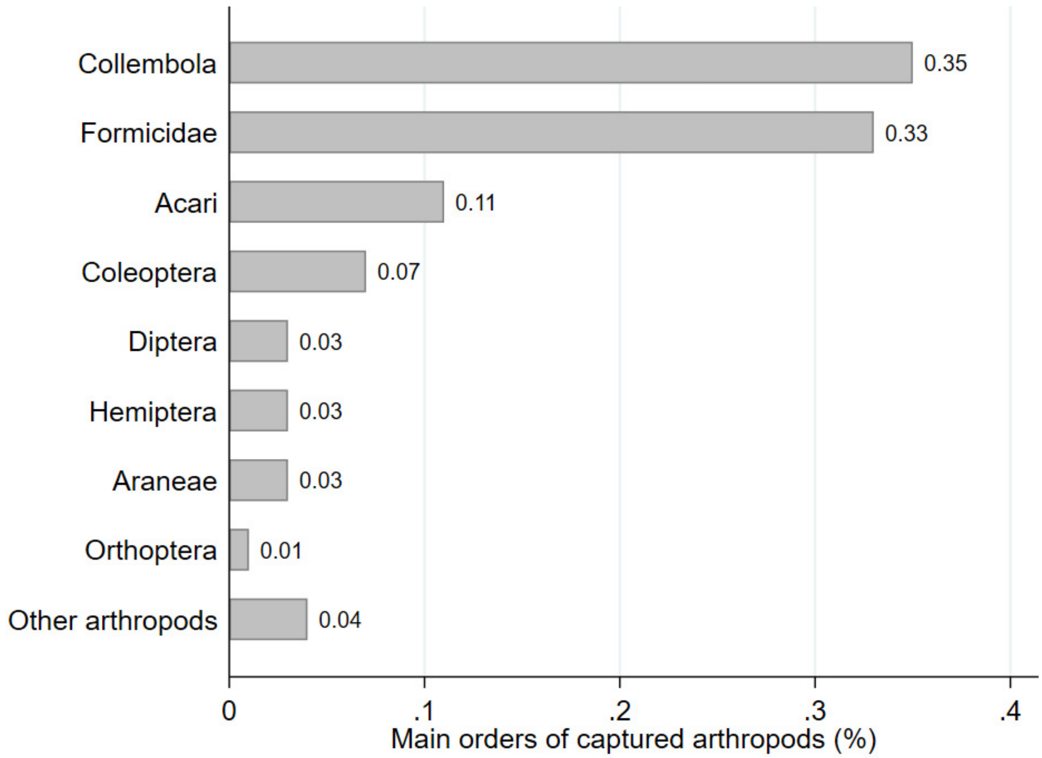

Fig 2. Identified arthropod orders in repeated captures in pitfall traps. El Mira Research Center, Tumaco, Pacific Coast of Colombia, 2017.

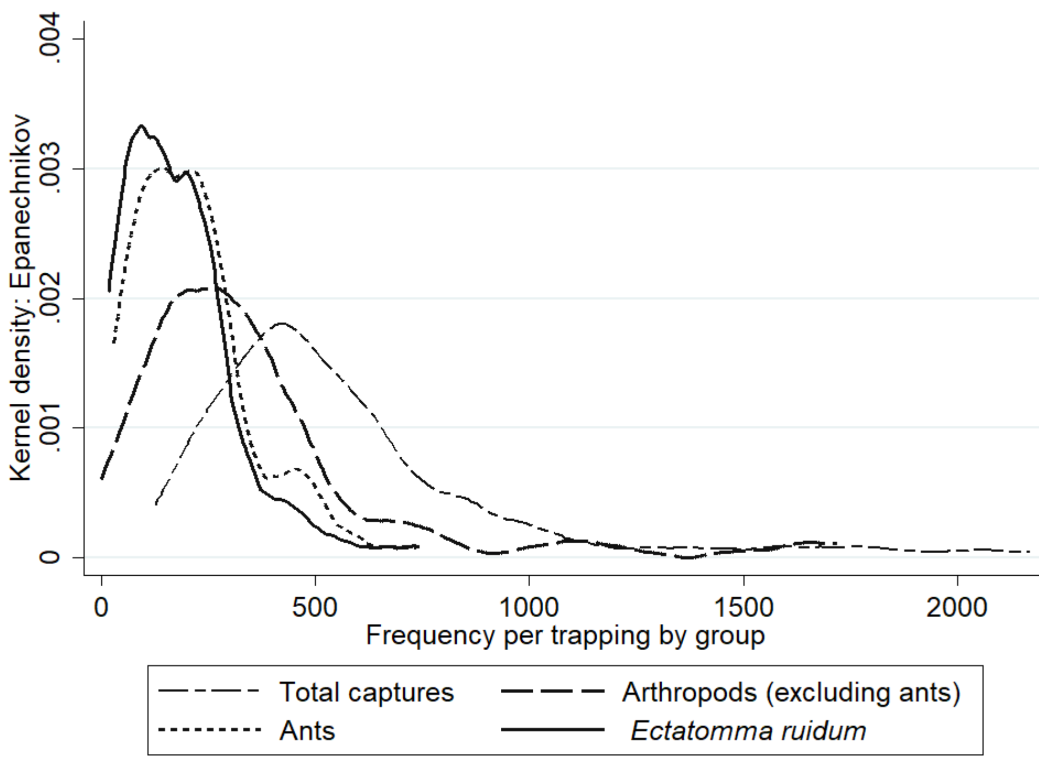

Fig 3. Density of total captured individuals per major group of analysis. El Mira Research Center, Tumaco, Pacific Coast of Colombia, 2017.

linear regression models that separately account for the overdispersion across groups.

Since the experiment was carried across different environments, we further explored differences in the dynamics of captures. First, plotting the observed captures on each round of trapping revealed that the data carried an important degree of variance (statistical overdispersion). The environments reported different patterns and data concentrations. As an example, the total *Ectatomma ruidum* captures were, on average, higher in both palm plots (4,616-6,697) than in the secondary forest (4,053) or the peach palm plantation (3,393) (see also Fig 4). Moreover, a multivariate analysis of variance (Table 1) reveals significant statistical differences among the captures in the different environments. We reject the null hypothesis of no-differences between plots on every test, further strengthening our argument for modeling the effects of pitfall trapping both by including fixed effects and at the plot level.

We summarize the results from Poisson regressions on Tables 2, 3, and 4, whereas those from NB2 models are reported in Tables 5, 6, and 7, providing details for non-ant arthropods, all ants, and *Ectatomma ruidum*. It is important to highlight how implementing both approaches reveals the offset to some significance after controlling for the data's high variance via the NB2 method. For example, if we had only followed the Poisson method, Table 2 would have suggested an apparent overall negative effect from trapping on all arthropods, and more specifically on the peach palm and seven y.o. oil-palm plantation. However, Table 5 shows that the NB2 approach attenuates such results, hence avoiding that coefficient estimates are affected due to high-variance (i.e., helps increase the efficiency of inferences). Therefore, our results suggest no effects of pitfall trapping over non-ant arthropods, neither at the aggregate level or plot-specific level.

On the other hand, although reduced in absolute value from one method to another, results regarding ants hold their sign and statistical significance. Initially, the overall effect

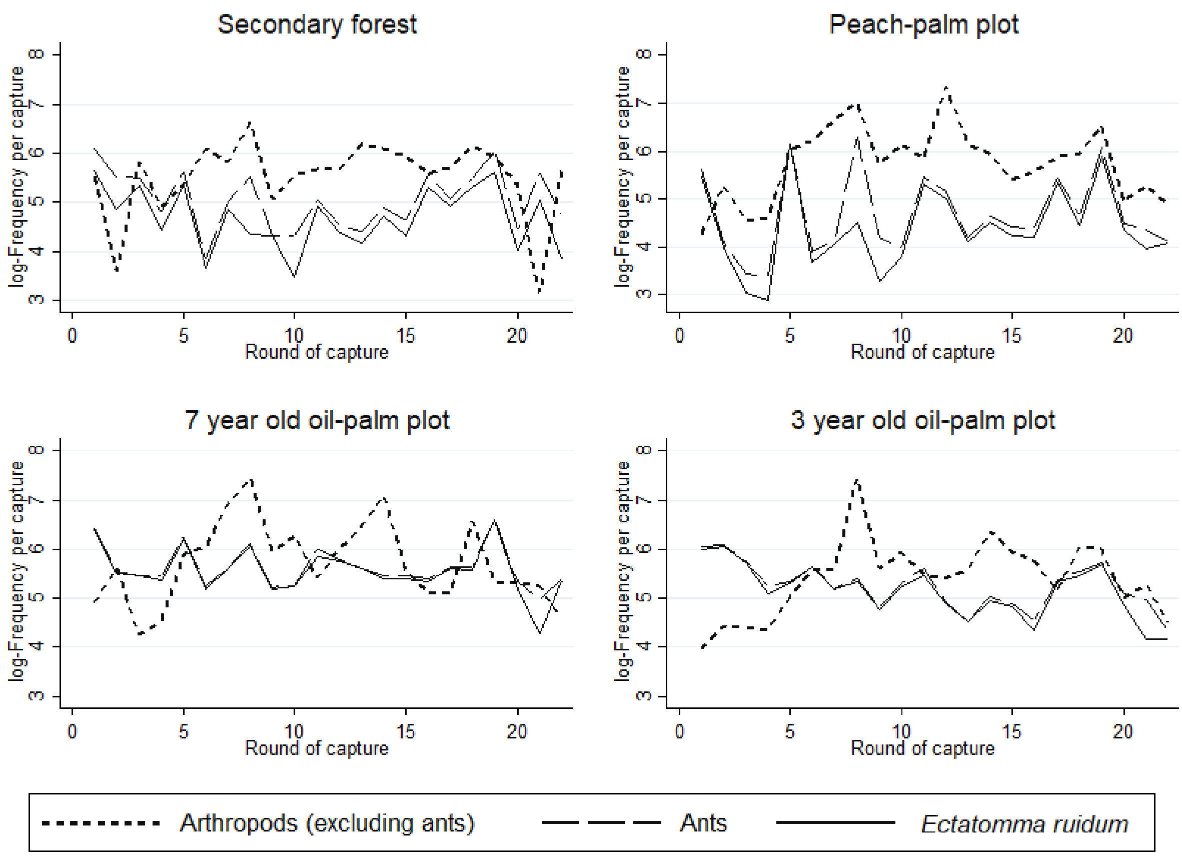

Fig 4. Log-frequency of captured ants, *Ectatomma ruidum*, and other arthropods in repeated captures in pitfall traps. El Mira Research Center, Tumaco, Pacific Coast of Colombia, 2017.

Table 1. Statistics of MANOVA for observed captures of non-ant arthropods, ants, and *Ectatomma ruidum* across plots.

Statistic	Estimate	df	*F*[df1 ; df2]	*F*-stat	*p*-value
Wilk's lambda	0.873	3	[9 ; 2107.8]	13.46	0.000***
Pillai's trace	0.129		[9 ; 2604.0]	12.99	0.000***
Lawley-Hotelling trace	0.143		[9 ; 2594.0]	13.8	0.000***
Roy's largest root	0.128		[3 ; 868.0]	37.16	0.000***

*** $p<0.001$; ** $p<0.005$; * $p<0.01$.

seems to be inexistent after controlling for climatic covariates. Nevertheless, Tables 3-4 reveal that on a Poisson setting, on average, each 24hrs trapping event implies a negative effect of -4.3% and -5.1% on subsequent captures of all ants and *Ectatomma ruidum*, respectively, specifically in the younger oil-palm plantation. These effects decrease (in absolute value) to -3.8% and -4.7% in the NB2 model. After further controlling for same-day solar radiation and precipitation, these effects slightly decreased to -3.0% and -3.9% in Poisson and -3.8% and -2.7% in the negative binomial specification. Thus, these results are robust and hold at a 0.05 level of significance.

Table 2. Estimated effect of pitfall trapping over non-ant arthropods by Poisson regression model.

	Response variable: Total captured individuals of non-ant arthopods									
Covariates	(1)[(a)]	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Round of capture (cumulative)	-0.012	-0.029***	-0.003	-0.011	-0.008	-0.032***	-0.027	-0.046**	-0.004	-0.018
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.03)
Capture after flooding	-0.937***	-0.425***	-0.752*	-0.435	-0.766***	-0.111	-1.128***	-0.623**	-1.143**	-0.567
	(0.14)	(0.13)	(0.28)	(0.27)	(0.22)	(0.26)	(0.22)	(0.20)	(0.37)	(0.23)
Solar radiation (W/m2)		-0.000***		0.000		-0.000***		-0.000*		-0.000
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Precipitation (mm)		-0.003***		-0.004***		-0.002		-0.003		-0.006
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Observations	872		220		219		217		216	
Method	Poisson		Poisson		Poisson		Poisson		Poisson	
Plot Fixed Effects	Yes		N/A		N/A		N/A		N/A	
Plot	N/A		Secondary forest		Peach palm		Oil-palms (7 years)		Oil-palms (3 years)	

(a) Each column presents the coefficients of regressing the response variable on the specific covariates, either including or excluding weather controls, under a *Poisson* model. Columns 1-2 pool the data and include plot-fixed effects, whereas the remaining columns report regression coefficients based on data from specific plots (see bottom of each column). Robust standard errors in parentheses. *** p<0.001, ** p<0.005, * p<0.01

Table 3. Estimated effect of pitfall trapping over all ants by Poisson regression model.

	Response variable: Total captured individuals of all ants									
Covariates	(1)[(a)]	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Round of capture (cumulative)	-0.023***	-0.012	-0.012	0.009	-0.015	-0.012	-0.019	-0.013	-0.043***	-0.030***
	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)
Capture after flooding	-0.162	-0.449***	-0.102	-0.606	-0.493	-0.604	-0.303	-0.495	0.122	-0.184
	(0.10)	(0.12)	(0.23)	(0.29)	(0.28)	(0.38)	(0.17)	(0.20)	(0.13)	(0.15)
Solar radiation (W/m2)		0.000		0.000**		0.000		0.000		0.000
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Precipitation (mm)		0.002***		0.003		0.001		0.001		0.002**
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Observations	872		220		219		217		216	
Method	Poisson		Poisson		Poisson		Poisson		Poisson	
Plot Fixed Effects	Yes		N/A		N/A		N/A		N/A	
Plot	N/A		Secondary forest		Peach palm		Oil-palms (7 years)		Oil-palms (3 years)	

(a) Each column presents the coefficients of regressing the response variable on the specific covariates, either including or excluding weather controls, under a *Poisson* model. Columns 1-2 pool the data and include plot-fixed effects, whereas the remaining columns report regression coefficients based on data from specific plots (see bottom of each column). Robust standard errors in parentheses. *** p<0.001, ** p<0.005, * p<0.01

Table 4. Estimated effect of pitfall trapping over *Ectatomma ruidum* by Poisson regression model.

	Response variable: Total captured individuals of Ectatomma ruidum									
Covariates	(1)[(a)]	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Round of capture (cumulative)	-0.026***	-0.014	-0.013	0.006	-0.005	0.009	-0.023	-0.016	-0.051***	-0.039***
	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)
Capture after flooding	-0.142	-0.435***	-0.161	-0.480	-0.262	-0.598	-0.315	-0.532	0.107	-0.202
	(0.10)	(0.12)	(0.23)	(0.28)	(0.28)	(0.42)	(0.18)	(0.22)	(0.14)	(0.17)
Solar radiation (W/m2)		0.000*		0.000***		0.000		0.000		0.000
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Precipitation (mm)		0.002**		0.001		0.002		0.001		0.002**
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Observations	872		220		219		217		216	
Method	Poisson		Poisson		Poisson		Poisson		Poisson	
Plot Fixed Effects	Yes		N/A		N/A		N/A		N/A	
Plot	N/A		Secondary forest		Peach palm		Oil-palms (7 years)		Oil-palms (3 years)	

(a) Each column presents the coefficients of regressing the response variable on the specific covariates, either including or excluding weather controls, under a *Poisson* model. Columns 1-2 pool the data and include plot-fixed effects, whereas the remaining columns report regression coefficients based on data from specific plots (see bottom of each column). Robust standard errors in parentheses. *** p<0.001, ** p<0.005, * p<0.01

There are statistically significant differences between captures that occur after flooding events and those performed on average weather conditions, specifically for non-ant arthropods. We found no effects of this kind for ants. Overall, non-ant pitfall catches after flooding events are expected to report about 39.1% of the captures that would have been found at normal conditions[3] under a Poisson distribution. After controlling for the observed solar radiation and daily precipitation on the series, the scale goes up to 65.3% (i.e., the effect is slightly half than that of the uncontrolled case). If a negative binomial distribution is assumed, these metrics change to 40.7% and 69.2%. Nonetheless, such effect only holds at the plot level in 7 yeas old oil-palm plantations, regardless of the statistical method. Conversely, flooding events do not seem to affect the expected number of ant-captures when analyzing the effect at the plot level.

Table 5. Estimated effect of pitfall trapping over non-ant arthropods by Negative Binomial (NB2) regression model.

	Response variable: Total captured individuals of non-ant arthopods									
Covariates	(1)[(a)]	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Round of capture (cumulative)	-0.006	-0.020	0.006	-0.004	-0.003	-0.022	-0.038	-0.042	0.004	-0.010
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.02)	(0.03)	(0.03)
Capture after flooding	-0.898***	-0.368*	-0.738**	-0.435	-0.735***	-0.049	-1.144***	-0.705**	-1.118***	-0.457
	(0.13)	(0.14)	(0.25)	(0.25)	(0.21)	(0.26)	(0.19)	(0.24)	(0.33)	(0.23)
Solar radiation (W/m2)		-0.000***		0.000		-0.000***		-0.000*		-0.000
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Precipitation (mm)		-0.003***		-0.005***		-0.002		-0.001		-0.003
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Observations	872		220		219		217		216	
Method	Poisson		Poisson		Poisson		Poisson		Poisson	
Plot Fixed Effects	Yes		N/A		N/A		N/A		N/A	
Plot	N/A		Secondary forest		Peach palm		Oil-palms (7 years)		Oil-palms (3 years)	

(a) Each column presents the coefficients of regressing the response variable on the specific covariates, either including or excluding weather controls, under a *Negative Binomial* (NB2) model. Columns 1-2 pool the data and include plot-fixed effects, whereas the remaining columns report regression coefficients based on data from specific plots (see bottom of each column). Robust standard errors in parentheses. *** p<0.001, ** p<0.005, * p<0.01

Table 6. Estimated effect of pitfall trapping over all ants by Negative Binomial (NB2) regression model.

	Response variable: Total captured individuals of all ants									
Covariates	(1)[(a)]	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Round of capture (cumulative)	-0.019***	-0.007	-0.010	0.015	-0.008	-0.005	-0.016	-0.011	-0.038***	-0.027**
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)
Capture after flooding	-0.122	-0.373***	-0.094	-0.578	-0.411	-0.451	-0.270	-0.391	0.156	-0.108
	(0.09)	(0.11)	(0.23)	(0.26)	(0.23)	(0.29)	(0.15)	(0.16)	(0.12)	(0.15)
Solar radiation (W/m2)		0.000		0.000**		0.000		0.000		0.000
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Precipitation (mm)		0.002**		0.003		0.000		0.001		0.002
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Observations	872		220		219		217		216	
Method	Poisson		Poisson		Poisson		Poisson		Poisson	
Plot Fixed Effects	Yes		N/A		N/A		N/A		N/A	
Plot	N/A		Secondary forest		Peach palm		Oil-palms (7 years)		Oil-palms (3 years)	

(a) Each column presents the coefficients of regressing the response variable on the specific covariates, either including or excluding weather controls, under a *Negative Binomial* (NB2) model. Columns 1-2 pool the data and include plot-fixed effects, whereas the remaining columns report regression coefficients based on data from specific plots (see bottom of each column). Robust standard errors in parentheses. *** p<0.001, ** p<0.005, * p<0.01

Table 7. Estimated effect of pitfall trapping over *Ectatomma ruidum* by Negative Binomial (NB2) regression model.

	Response variable: Total captured individuals of Ectatomma ruidum									
Covariates	(1)[(a)]	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Round of capture (cumulative)	-0.020**	-0.004	-0.010	0.011	-0.000	0.029	-0.020	-0.014	-0.047***	-0.038***
	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)
Capture after flooding	-0.077	-0.352**	-0.137	-0.472	-0.241	-0.605	-0.269	-0.400	0.164	-0.081
	(0.10)	(0.12)	(0.22)	(0.27)	(0.23)	(0.30)	(0.16)	(0.18)	(0.12)	(0.16)
Solar radiation (W/m2)		0.000**		0.000***		0.000		0.000		0.000
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Precipitation (mm)		0.002**		0.001		0.002		0.001		0.002
		(0.00)		(0.00)		(0.00)		(0.00)		(0.00)
Observations	872		220		219		217		216	
Method	Poisson		Poisson		Poisson		Poisson		Poisson	
Plot Fixed Effects	Yes		N/A		N/A		N/A		N/A	
Plot	N/A		Secondary forest		Peach palm		Oil-palms (7 years)		Oil-palms (3 years)	

(a) Each column presents the coefficients of regressing the response variable on the specific covariates, either including or excluding weather controls, under a *Negative Binomial* (NB2) model. Columns 1-2 pool the data and include plot-fixed effects, whereas the remaining columns report regression coefficients based on data from specific plots (see bottom of each column). Robust standard errors in parentheses. *** p<0.001, ** p<0.005, * p<0.01

Discussion

Theory suggests epigeal pitfall trapping may significantly affect the populations of ground-active arthropods. Greenslade (1973) warns about three specific digging-in effects that might influence captures when sampling ants and likely confound estimates of pitfall-trapping effects. These are: (a) penetration of nest galleries, (b) traps located between nests and food sources, and (c) ants exploring new features in their territories. Using a dataset from a study in Southwestern Colombia, we circumvent the likelihood of such confounding effects to provide an unbiased and precise measure of pitfall trapping effects, specifically for *Ectatomma ruidum*. We have two main arguments for this purpose. First, the largest share of captured ants was of *E. ruidum* (>87%), and traps were small in height (60 mm) and widely distributed across the plots. *Ectatomma ruidum* nests are usually single-entrance vertical galleries (Franz & Wcislo, 2003), located at a medium depth of 35 cm (Armbrecht & Santamaría, personal communication, June 21, 2019). Moreover, this species does not follow specific trails while foraging (Franz & Wcislo, 2003). Thus, it is an acceptable assumption to consider that confounders (a) and (b) do not apply. Second, when considering the duration of the study (one year) and the specifics of *Ectatomma ruidum* behavior, it is simple to rule out any relation with confounder (c) and with the case of higher initial captures due to increased CO_2.

Whereas there are cases like Slezák et al. (2010), which reported a drastic reduction of carabid and diplopod numbers in the second year after one year of pitfall sampling and attributed the difference to over-catching in the first year, their traps were installed and actively collected specimens throughout the season. This study's sampling was limited to two periods of 24 hours of trapping per month, hence – third, and finally – ruling out short-term digging-in effects and making a stronger case of any detected impact to be defined as of depletion of populations. This also complies with the data, which shows that the decrease in captures is not systematically seen only at first capture events; conversely, it is observed only in the long-term. Our results are made further robust by including weather controls (solar radiation and precipitation), as well as extreme variability shocks, namely floodings. The latter seems to affect non-ant arthropods' captures systematically, but no effect is found either on all ants or *Ectatomma ruidum*. As of why *Ectatomma ruidum* is not affected by these flooding events, this likely follows from their vertical, single-entrance, deep nests, as well as their trait of distributing across several small colonies instead of a single nest (Franz & Wcislo, 2003; Armbrecht & Santamaría, personal communication, June 21, 2019). In brief, since the analysis relies on low-intensity trapping data with important exogenous controls, we consider this an estimate of a lower boundary of such an effect. Therefore, if the effect is detected even with fortnightly events, this is a minimum effect attributed to pitfall trapping in the absence of confounding events.

Besides, there were important differences in total ant – and *Ectatomma ruidum* – captures across the four different plots, representing different levels of disturbance. Following the findings of Jiménez-Carmona et al. (2019), this is of importance. Habitat specifics might influence differences in detected digging-in effects. The dominance of *Ectatomma ruidum* in the oil palm plots can be explained as these are highly disturbed environments where scarcity of food sources is a common issue. *Ectatomma ruidum*, as a generalist forager (Franz & Wcislo, 2003; Lachaud, 1990), has a definitive advantage over more specialized ant species. However, as the data show, they are vulnerable to activities like pitfall trapping, which has measurably reduced their numbers with each subsequent capture. An explanation to this finding is the small size of the colonies, which are about 50-150 individuals (Franz & Wcislo, 2003). If 20% of the ants of any colony are engaged in foraging, each colony may have just 10 - 40 active foragers. Yet, the average number of individuals caught per trapping occasion in the oil palm plots went up to 30 individuals. This could have had a significant impact on the amount of food gathered and, thus, on colony maintenance and growth.

In summary, results suggest that although overall arthropods' captures were stable through time, plot-level analyses indicate that, on average, each additional capture significantly reduced the overall population of ants – specifically *Ectatomma ruidum* – in some plots. This species is characterized by numerous, small colonies with a limited number of foragers, which even low-intensity pitfall trapping can affect by repeated removal of a large proportion of the active foragers. Even though this is a case study, this result might be important for future studies that rely on this method to deliver consistent estimates of their population sizes or their dynamics through time since the possibility of a biased estimation is latent by the factors here explored.

Disclaimer

The authors agree with this article's publication and declare no conflicts of interest that affect the results.

Note

[1] Cameron & Trivedi (2005, 2009) show that setting the density of ν as $g(\nu) = \frac{\nu^{\delta-1} e^{-\nu\delta} \delta^{\delta}}{\Gamma(\delta)}$, yields the negative binomial distribution that possesses a mixture density $h[y|\mu,\delta] = \frac{\Gamma(\alpha^{-1}+y)}{\Gamma(\alpha^{-1})\Gamma(y+1)} \left(\frac{\alpha^{-1}}{\alpha^{-1}+\mu}\right)^{\alpha^{-1}} \left(\frac{\mu}{\mu+\alpha^{-1}}\right)^{y}$ where $\alpha = 1/\delta$.

[2] We tested for non-normality (not included here) and found that there are strong differences in which the mean value is statistically larger than the median. For example, mean and median captures were (577; 489.5), (363.9; 274), and (213.1; 195) for all captures, non-ant captures, and ant captures, respectively.

[3] Due to the magnitude of the detected effect of captures-after-flooding, the best interpretation of this coefficient is the scale difference $\exp(\beta_2)$ (Cameron & Trivedi, 2009). For small effects, the semi-elasticity interpretation holds since it is symmetric to the scale change.

References

Adis, J. (1979). Problems of interpreting arthropod sampling with pitfall traps. Zoologischer Anzeiger, 202: 177-184.

Brown, G.R. & Matthews, I.M. (2016). A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. Ecology and Evolution, 6: 3953-64. doi: 10.1002/ece3.2176

Cameron, A.C. & Trivedi, P.K. (2005). Microeconometrics: Methods and Applications. Cambridge University Press. Cambridge, UK.

Cameron, A.C. & Trivedi, P. K. (2009). Microeconometrics using Stata. The Stata Press. College Station, TX.

Franz N.M. & Wcislo, T. (2003). Foraging Behavior in Two Species of *Ectatomma* (Formicidae: Ponerinae): Individual Learning of Orientation and Timing. Journal of Insect Behaviour, 16: 381-410. doi: 10.1023/A:1024880110189

Gist, C.S. & Crossley, J.R (1973). A Method for Quantifying Pitfall Trapping. Environmental Entomology, 2: 951-52. doi: 10.1093/ee/2.5.951

Greene, W.H. (2012). Econometric Analysis, 7th ed. Prentice-Hall. Upper Saddle River, NJ.

Greenslade, P.J.M. (1964). Pitfall Trapping as a Method for Studying Populations of Carabidae (Coleoptera). Journal of Animal Ecology, 33: 301-10. doi: 10.2307/2632

Greenslade, P.J.M. (1973). Sampling ants with pitfall traps: Digging-in effects. Insectes Sociaux, 20: 343-53. doi: 10.1007/BF02226087

Hayes, W.B. (1970). The Accuracy of Pitfall Trapping for the Sand-Beach Isopod *Tylos punctatus*. Ecology, 51: 514-16. doi: 10.2307/1935388

Jansen, M.J.W. & Metz, J.A.J. (1979). How many victims will a pitfall make? Acta Biotheoretica, 28: 98-122. doi: 10.1007/BF00046807

Jiménez-Carmona, F., Carpintero, S. & Reyes-López, J.L. (2019). The digging-in effect on ant studies with pitfall traps: influence of type of habitat and sampling time. Entomologia Experimentalis et Applicata, 167: 906-14. doi: 10.1111/eea.12834

Joosse, E.N.G. (1965). Pitfall-trapping as a method for studying surface dwelling collembola. Zeitschrift für Morphologie und Ökologie der Tiere, 55: 587-96. doi: 10.1007/BF00407477

Joosse, E.N.G. & Kapteijn, J.M. (1968). Activity-stimulating phenomena caused by field-disturbance in the use of pitfall-traps. Oecologia, 1: 385-92. doi: 10.1007/BF00386692

Lachaud, J.P. (1990). Foraging activity and diet in some neotropical ponerine ants. I. *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). Folia Entomológica Mexicana, 78: 241-56.

Lasmar, C.J., Queiroz, A.C.M., Rabello, A.M., Feitosa, R.M., Canedo-Júnior, E.O., Schmidt, F.A., Cuissi, R.G. & Ribas, C.R. (2017). Testing the effect of pitfall-trap installation on ant sampling. Insectes Sociaux, 64: 445-51. doi: 10.1007/s00040-017-0558-7

Löhr, B.L. & Narváez, C.A. (2021). Land use and terrestrial arthropods at the Colombian Pacific coast. Revista Colombiana de Entomología, 47: e7640. doi: 10.25100/socolen.v47i1.7640

Luff, M.L. (1975). Some Features Influencing the Efficiency of Pitfall Traps. Oecologica, 19: 345-57. doi: 10.1007/BF00348110

Reyes, C.R. (2012). Respuesta fisiológica de la palma aceitera (*Elaeis guineensis* Jacq.) a la disponibilidad de agua en el suelo. PhD Thesis. Universidad de Costa Rica. San José de Costa Rica. 210 p.

Santamaría, C., Armbrecht, I. & Lachaud, J.P. (2009). Nest Distribution and Food Preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in Shaded and Open Cattle Pastures of Colombia. Sociobiology, 53: 517-541.

Schirmel, J., Lenze, S., Katzmann, D. & Buchholz, S. (2010). Capture efficiency of pitfall traps is highly affected by sampling interval. Entomologia Experimentalis et Applicata, 136: 206-10. doi: 10.1111/j.1570-7458.2010.01020.x

Sheikh, A.H., Ganaie, G.A., Thomas, M., Bhandari, R. & Rather Y.A. (2018). Ant pitfall trap sampling: An overview. Journal of Entomological Research, 42: 421-36. doi: 10.5958/0974-4576.2018.00072.5

Slezák, V., Hora, P. & Tuf, I.H. (2010). Effect of pitfall-trapping on the abundance of epigeic macrofauna – preliminary results. Acta Societatis Zoologicae Bohemicae 74:129-33.

Stevens, J.P. (2002). Applied multivariate statistics for the social sciences. Mahwah, NJ: Lawrence Erblaum.

Southwood, T.R.E. (1978). Ecological Methods: with particular reference to the study of insect populations, 2nd ed. Springer. Heidelberg, Germany.

Southwood, T.R.E. & Henderson, P.A. (2016). Ecological Methods, 4th ed. Wiley-Blackwell. Hoboken, NJ.