Low impact of anthropization on the demographic structure of the stick insect *Clonistria guadeloupensis* in Guadeloupe

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Abstract

Mitigating the biodiversity crisis will require an understanding of how species cope with various human disturbances of habitats ranging from fully natural environments to areas with higher anthropization levels. In this study, we investigated how the local demographics of *Clonistria guadeloupensis* (Redtenbacher) relate to human disturbances such as agricultural fields, roads, and urbanization in Guadeloupe. We sampled the species in diverse environmental situations in the wild, both on and around focal food plants, and recorded the habitat characteristics. We subsequently analyzed the demography of the juvenile, subadult, and adult stages. We found minimal impact of anthropization factors, with a tendency of the species to be associated with habitats with greater anthropization levels, possibly because such habitats are generally more open. We also found variation in local aggregation levels of the developmental stages, which may reflect bias in dispersal during the adult stage in which males are highly motile. Overall, the species shows ecological preferences appropriate for coexistence within areas of human disturbance.

Keywords

Agriculture, habitat disturbance, human wildlife coexistence, road, stick insects, urbanization

Introduction

The ongoing biodiversity crisis is among the most important challenges of this century (Cardinale et al. 2012, O'Connor et al. 2020). Indeed, human activities have considerably reduced the amount of space available for wildlife, and the current rate of species extinction has raised concerns about protecting nature and preventing further losses in species diversity (Tilman et al. 2017). However, the impact of human activity is often asymmetrical, as some species are adapting to new ecological niches created by human expansion, including urbanized habitats (McDonnell and Hahs 2015, Vrbanec et al. 2021). Recent scientific debates have arisen over which approach to the biodiversity crisis would lead to greater conservation benefits, such as whether agriculture should be intensified so as to decrease cultivated surface and thus free space devoted to wildlife, or made more extensive so as to create natural–anthropized continuums where both human activity and wildlife can coexist (Whittaker et al. 2005, Baudron and Giller 2014, Loconto et al. 2020). Thus, the study of species distribution in both untouched primal areas and anthropized habitats is relevant to the issues of diversity and conservation (Elphick 2000, Brand and Snodgrass 2010).

Some conservation studies have shown bias toward species that humans most closely identify with, a process known as 'vertebrate bias' (Titley et al. 2017, Davies et al. 2018, Raja et al. 2022). This bias is present in both choices for natural reserves and in the study of anthropized habitats (Dearborn and Kark 2010), with less research being done on animals such as insects despite recent renewed interest in pollinators and the service they provide (Hall et al. 2017, Wenzel et al. 2020, Ayers and Rehan 2021). It is important to reduce this gap in the knowledge to better assess the impact of anthropization gradients, especially regarding insect diversity (Diamond et al. 2022).

The anthropization levels of degraded environments are known to impact insects, usually negatively (Fenoglio et al. 2020, Collins et al. 2024), depending on ecological specialization of species (Rocha and Fellowes 2020, Perez et al. 2022), the impact of nature-management in urban areas (Sanetra et al. 2024), and the insect order itself (Sempe et al. 2024). This implies a need to understand how increased human disturbances in already-anthropized areas affect insect populations as they adapt to the new environments (Diamond et al. 2022, 2023).

Increasing urbanization has a triple impact on biodiversity. First, it may be beneficial by creating habitats ready for colonization by wild species in places that were previously different in nature or unsuitable (Fattorini 2016, Fenoglio et al. 2021), although this usually favors more cosmopolitan species (Adams et al. 2020) and the dynamics will depend on the local carrying capacity of the urban niches. Second, increasing urbanization can disrupt dispersal paths and increase population isolation (Barr et al. 2021), sometimes leading to strict delineation of habitats and lower diversity among low dispersers (Muñoz et al. 2015). The same pattern is seen with roads, which can both mediate dispersal (Andersson et al. 2017) or reduce population size (Martin et al. 2018, Bhardwaj et al. 2019), with intensity depending on local road management (e.g., New et al. 2021). Third, intensive agriculture, as part of increased urbanization, is a major driver of insect loss worldwide (Raven and Wagner 2021, Uhler et al. 2021, Powell et al. 2024), mostly due to the chemical control of crop pests. These three disturbances can impact local fauna at various levels (González-Césped et al. 2021), especially in the Caribbean islands where the constraint of insularity makes the anthropization continuum somewhat abrupt in terms of gradation.

In this study, we focused on a nocturnal and locally common species of stick insect, *Clonistria guadeloupensis* Redtenbacher, 1908, to investigate the impact of environmental anthropization on demographics and dispersal. We delineated the effects of agricultural activity (distance from sample to first fields) and human occupancy (distance from sample to first buildings and roads, respectively) and used statistical analysis to determine whether these disturbances impacted the number of juveniles, subadults and adults and the adult sex ratio. Our aim was to describe the effect of these disturbances on a relatively generalist species with moderate dispersal ability and to determine the species' potential for establishment in anthropised and degraded environments.

Materials and methods

Study species.—Clonistria guadeloupensis is a slender stick insect species found throughout Guadeloupe and its dependencies, both in wet, tropical forests and xeric, degraded habitats (Lelong and Langlois 2001). The species was initially split into two putative species based on ecological specialization (ecotypes): *C. guadeloupensis sensu stricto*, found in hygrophilic forests, and a yet undescribed *Clonistria* sp., found in more xeric environments. The species (or morphs) were distinguished primarily based on size, with *C. guadeloupensis* being larger in size. Recent investigations have proposed a status of species complex due to inconsistencies in the body size delineation criterion and range, as there is significant overlap between the hygrophilic and mesophilic forms (Jourdan et al. 2023). This species complex is found in a wide array of habitats in both undisturbed and anthropized areas and is known to feed on wild vegetation and plant species associated with human crops (e.g., guava, pigeon peas, etc.). Adults and subadults are easily sexed as the species is sexually dimorphic.

The genus *Clonistria* Stål, 1875 is widely represented in the Caribbean, ranging from Southern to North Antilles (Langlois and Lelong 2005, 2010), although current species delineations are unclear even at the local level and likely require taxonomic revision at the Caribbean scale. Indeed, larger *Clonistria* species have recently been assigned to newly created genera (Bellanger et al. 2023), and clarifications of smaller-sized species are pending. Biogeographically speaking, the Caribbean Basin is considered a biodiversity hotspot (Maunder et al. 2008), both because of the archipelago nature of the island range and, locally, because of volcanic mountains differentiating niches and environments with potential consequences for speciation (Bellanger et al. 2021) and species dispersal (Shapiro et al. 2022).

Sampling and data recording.—Primary study areas were randomly assigned throughout the Basse Terre and Grande Terre regions (humid and dry, respectively) in Guadeloupe from within the natural range of *C. guadeloupensis* (Fig. 1). Eleven study areas were subsequently chosen as prospective sampling spots. Paths in natural vegetation were walked through until a specimen was observed. The location of the specimen was defined as a sample study spot provided that the previous spot was more than 20 m away (most sample spots were greater than 20 m away from the previous spot). Once a spot was defined, every specimen on the focal food plant was recorded and assigned its demographic category (juvenile, subadult, or adult for both sexes). Then, all specimens within 2 m of the initial focal food plant were recorded in the same way. Demographics were thus differentiated between the insects found on the focal sample food plant and those found around the focal plant. For each spot, sex ratio was calculated as the number of females over the number of adults for all sexed individuals (i.e., both adults and subadults). The local aggregation structure was calculated as the ratio of specimens within 2 m of the spot over the total number of sample specimens found ((ranging from zero, i.e., full aggregation, to 1, i.e., hints of local dispersal)) for each developmental stage (juveniles, subadults, and adults). Anthropization levels were estimated via three parameters: distance (in meters) to the first road (hereafter, 'Road'), to the first building/construction (hereafter, 'Building') and to the first cultivated field (hereafter, 'Field'). If a distance was greater than 100 m, it was reported as 100 m (truncation threshold).

Statistical analyses.—A principal component analysis was performed to investigate correlations between covariates and explore the potential clustering of spots with similarity in values. We log-transformed demographic data prior to analysis to increase the normality of distribution. We then ran ANCOVA analyses successively using total demographics and each demographic category as the independent and anthropization factors (Road, Building, Field) as dependents to assess the anthropic impact on species demographics. The intention was to study the impact of each disturbance on specific demographics; while we expected the disturbances to have a negative impact on *Clonistria guadeloupensis*, we approached our analyses with an open mind.

Our models are based on the 43 study spots, yielding an average of ca. 11 estimates per factor (4 factors per model), which is at the low end of sampling power for analysis of covariance; we decided to include Altitude as a covariate to increase precision on variance estimates for each of the disturbances. Subadults were the least common, and none of the factors were found to impact this developmental stage, possibly due to lower variation in individuals at this stage overall, so this model was not subjected to further analysis. The conditions of homoscedasticity and normality of residuals were met in all analyses. All analyses were done using R software (R Core Team 2021).

Results

From January to February 2020, a total of 163 *Clonistria guadeloupensis* were sampled from 43 study spots (3.79 ± 4.04 insects per spot, range 1–23). Among them, 76 were juveniles (1.77 ± 3.06 insects per spot, range 0–17), 21 were subadults (0.49 ± 0.87 insects per spot, range 0–4), and 66 were adults (1.53 ± 1.3 insects per spot, range 0–5). Among insects that could be sexed (subadults and adults), 43 were male (1.00 ± 1.25 insects per spot, range 0–5), and 25 were female (0.56 ± 0.66 insects per spot, range 0–2). The sex ratio among spots varied (0.35 ± 0.43, range 0–1). The individuals sampled within two meters from focal plant (F2m) ratios (local aggregation indices) were 0.59 ± 0.49 for adults, 0.08 ± 0.24 for subadults, and 0.18 ± 0.32 for juveniles; thus, juveniles were approximately three times more aggregated locally than adults on average.

Overview and clustering of data.—A principal component analysis demonstrated no aggregation of demographic and plot characteristics but rather a general spread, suggesting that sampling occurred on a continuum across anthropization gradients and that anthropization only had a weak effect on population structure (Fig. 2). Anthropization factors and altitude anticorrelated to most demographic stages, suggesting that the species is generally found at higher demographics when closer in proximity to anthropized habitats and that density decreases with altitude. However, the demographic components of the population structure were associated with open and xeric habitats overall.

The demographics of the species overall most closely resembled those of the juvenile stage, an expected pattern for a species in which females leave their eggs in feeding patches and usually demonstrate little mobility during adulthood. Indeed, hatching will typically take place around feeding sites, with higher emergence near food plants, resulting in juveniles driving total demographics locally. In contrast, subadult and adult demographics were less correlated with total demographics, and while subadult demographics were anticorrelated to anthropization factors, the situation somewhat reversed in adults, suggesting that dispersal-based effects occur between these stages.

For juveniles and subadults, demographics and F2m ratios were highly correlated, suggesting local aggregation patterns relevant to feeding behavior, while for adults, demographics and F2m ratio only slightly correlated, and F2m ratio strongly correlated to sex ratio, suggesting that aggregation level was much lower in adults and associated with local asymmetries in sex. Since females are known to have relatively low mobility as adults, these results suggest that the males are the higher dispersing sex in the species, a phenomenon suspected for Phasmatodea as males are more frequently observed during local citizen science participatory initiatives (T. Jourdan, personal observation).

Our analysis revealed demographics for each development stage to be anticorrelated to altitude (Fig. 2), which should be interpreted as an artifact of sampling rather than a causal process. Indeed, altitude is associated with tropical humid rainforest in Guadeloupe and is thus both much less subject to anthropization and an environmental niche for *C. guadeloupensis*. As a result, individuals are, in general, more interspersed in natural forest than they are in disturbed or degraded environments. This effect was significant for total demographics and marginally significant for juveniles but not significant for adults (Table 1), suggesting that the dilution effect was true as a general tendency, most markedly so for young

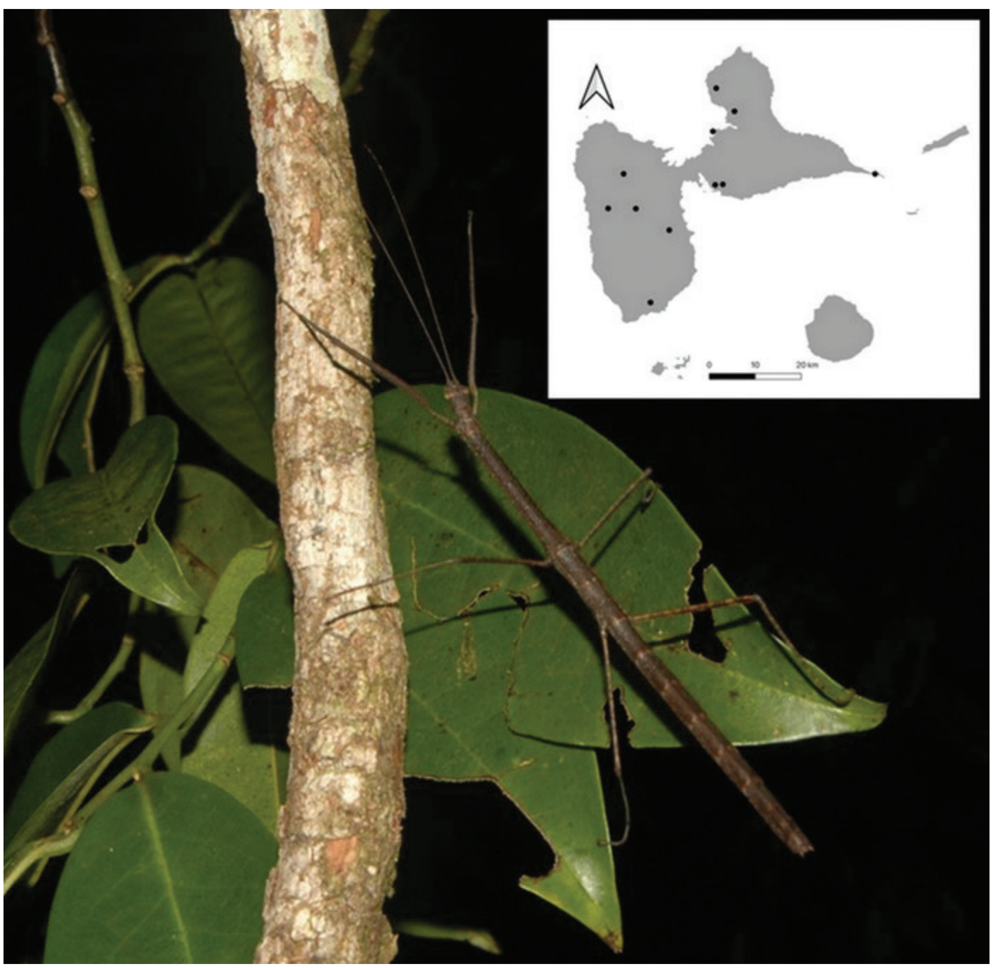

Fig. 1. *Clonistria guadeloupensis*, adult female, and geographic distribution of the study's primary sample areas.

insects. Overall, and for each development stage, anthropization factors had little impact on demographics (Table 1, Fig. 3A–D).

ANCOVA models.—Total population was significantly impacted by altitude (Table 1), with a decrease as altitude increased (Fig. 3A). It was also similarly impacted by 'Distance to road' (Fig. 3B), though at a marginally significant level (Table 1). The adult population was significantly impacted by 'Distance to agriculture field' (Table 1), with a fairly weak increase on the number of specimens sampled as distance from fields increased (Fig. 3C). Juvenile number were significantly impacted by 'Altitude' (Table 1), with a fairly weak increase on the number of specimens sampled as altitude increased (Fig. 3D). Despite the small size of the effects, the different models suggest a greater presence of *C. guadeloupensis* at a closer proximity to anthropized areas, possibly as a result of the species' attraction to more open and drier areas.

Discussion

This study found that anthropization disturbance levels had no significant impact on the demographics of *C. guadeloupensis* at all developmental stages, with a pattern of increased population size associated with greater anthropization of the environment. Aggregation levels were found to change based on developmental stage, decreasing from juvenile to adult. Aggregation level also strongly correlated with sex ratio, indicating a connection between variation in sex distribution and dispersal in adults, with males as the sexual dispersers (an observation corroborated by citizen science). These results are further discussed below as they relate to the consequences for the species.

Table 1. ANCOVA models of local population size for total population, adult insects, and juveniles with three anthropization factors (distance to agriculture area, distance to first human building, distance to road) and altitude and sex ratio as covariates. Significant model effects are in bold, and marginally significant effects in italics. Scale of significance is the following: 0 < '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1 < ' ' < 1.

Model	Df	Sum of Squares	Mean Square	F value	P (>F)
Total Population					
Altitude	1	2.457	2.457	6.534	0.0147 *
Agriculture	1	0.022	0.0220	0.058	0.8102
Building	1	0.183	0.1827	0.486	0.4900
Road	1	1.244	1.2443	3.310	0.0768 .
Residuals	38	14.287	0.3760		
Adults					
Altitude	1	0.136	0.136	0.522	0.4744
Agriculture	1	1.503	1.5025	5.758	0.0214 *
Building	1	0.033	0.0334	0.128	0.7224
Road	1	0.059	0.0587	0.225	0.6379
Residuals	38	9.916	0.2609		
Juveniles					
Altitude	1	2.733	2.733	4.840	0.034 *
Agriculture	1	0.168	0.168	0.297	0.589
Building	1	0.004	0.004	0.007	0.936
Road	1	1.465	1.465	2.594	0.116
Residuals	38	21.455	0.5646		

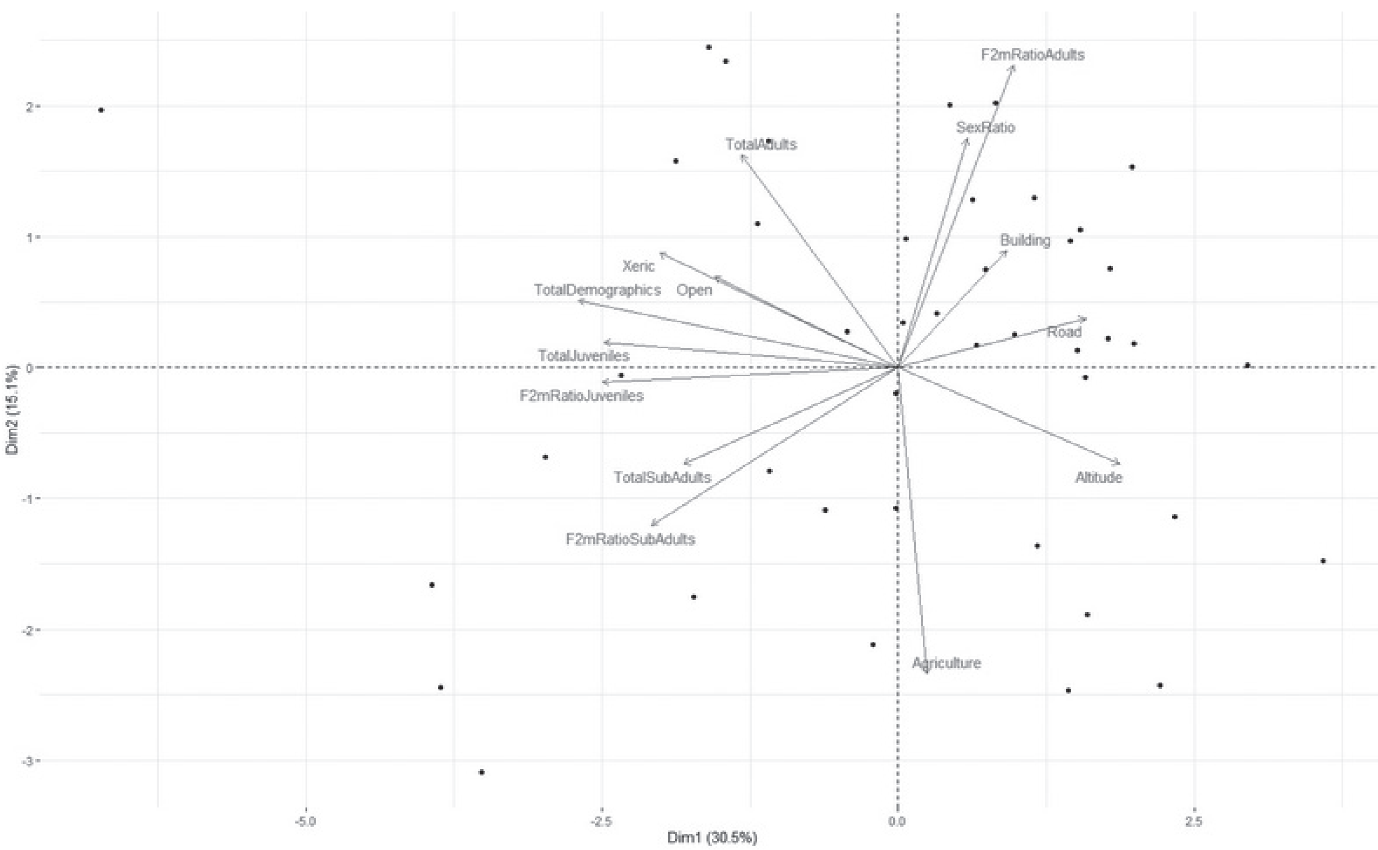

Fig. 2. Principal component analysis (PCA) of the demographic structure of *Clonistria guadeloupensis* in anthropized habitat gradients. The first axis retains 30.5% of variance and the second axis retains 15.1%, meaning nearly half of the data variance is retained in both axes. Ecological and demographic vectors are indicated in grey.

Overall, *C. guadeloupensis* has a propensity to live in xeric spaces with open vegetation, and open vegetation facilitates dispersal in insects, at least locally (Popović and Nowicki 2023). Interestingly, the anticorrelation between sex ratio and proximity to agriculture (Fig. 2) suggests that males of the species are more sensitive to this anthropization factor, possibly because agriculture is often associated with the presence of food plants (e.g., guava bushes growing at the edge of a crop field), a phenomenon already identified in several stick insect species in Guadeloupe (Jourdan et al. 2023).

Conversely, altitude was anticorrelated to local demographics in general, with fewer individuals sampled as elevation increased. In Guadeloupe, the environment becomes more forested at higher altitudes, and the species' demographics become spatially more continuous and occurring less patchily over focal plants (sampling was also made more difficult, as adults may spend more time in the forest canopy, although the effect of altitude on adult demographics was not significant). Thus, populations become both sparser and distributed more evenly in the environment (however, forested environments are also quite conducive to dispersal; see Cooke 2022). This contrast should be the focus of further study in order to investigate whether genetic structure is also impacted by altitude in our situation, as has been demonstrated in other species (Butterworth et al. 2023).

Local aggregation was strong in juveniles, even stronger in subadults, and decreased in adults, suggesting that subadults were highly focused on feeding behavior (and thus nearly always found on focal food plants) and adults were oriented toward reproductive behavior involving active dispersal, as local sex ratio was strongly associated with aggregation ratio. Food plants availability is known to impact insect aggregation (Jing et al. 2022), as are spaces of open vegetation (Evangelista et al. 2022), possibly as these locations increase mating success (Montes et al. 2022). The strong level of aggregation in juveniles could reflect the younger insects' tendency to stop exploring once settled on a food plant.

Overall, our results illustrate a pattern of increased demographics at proximity to anthropized habitats as a tendency for the species, possibly because of its preference for more-open habitats. Thus, *C. guadeloupensis* may be found in areas of high anthropization disturbances, such as roads and agricultural fields. It is seldom seen in urban settings (and when it is, it is usually the male that is sighted), likely as a result of a lack of food plant patches, but other habitats in Guadeloupe suit the species, and it occurs throughout. The importance of open vegetation is highlighting the importance such places for the colonization of unoccupied patches, and the species' occurrence in proximity to anthropized places may result in increasing the species' available range. Yet little is currently known about mobility and dispersal ability in stick insects in general beyond a pattern of greater male dispersal. Passive ecological migration via predation by birds has been hypothesized (Suetsugu et al. 2018), but evidence that this drives establishment of populations regionally, between or within islands, is lacking. Active dispersal following demographic increase and local overpopulation might be an interesting alternative hypothesis (i.e., individuals may disperse more when food availability decreases or is too low to sustain local demographics). Further investigation should focus on dispersal and migration in addition to testing the probability of migration success in open- vs. closed-vegetation environments.

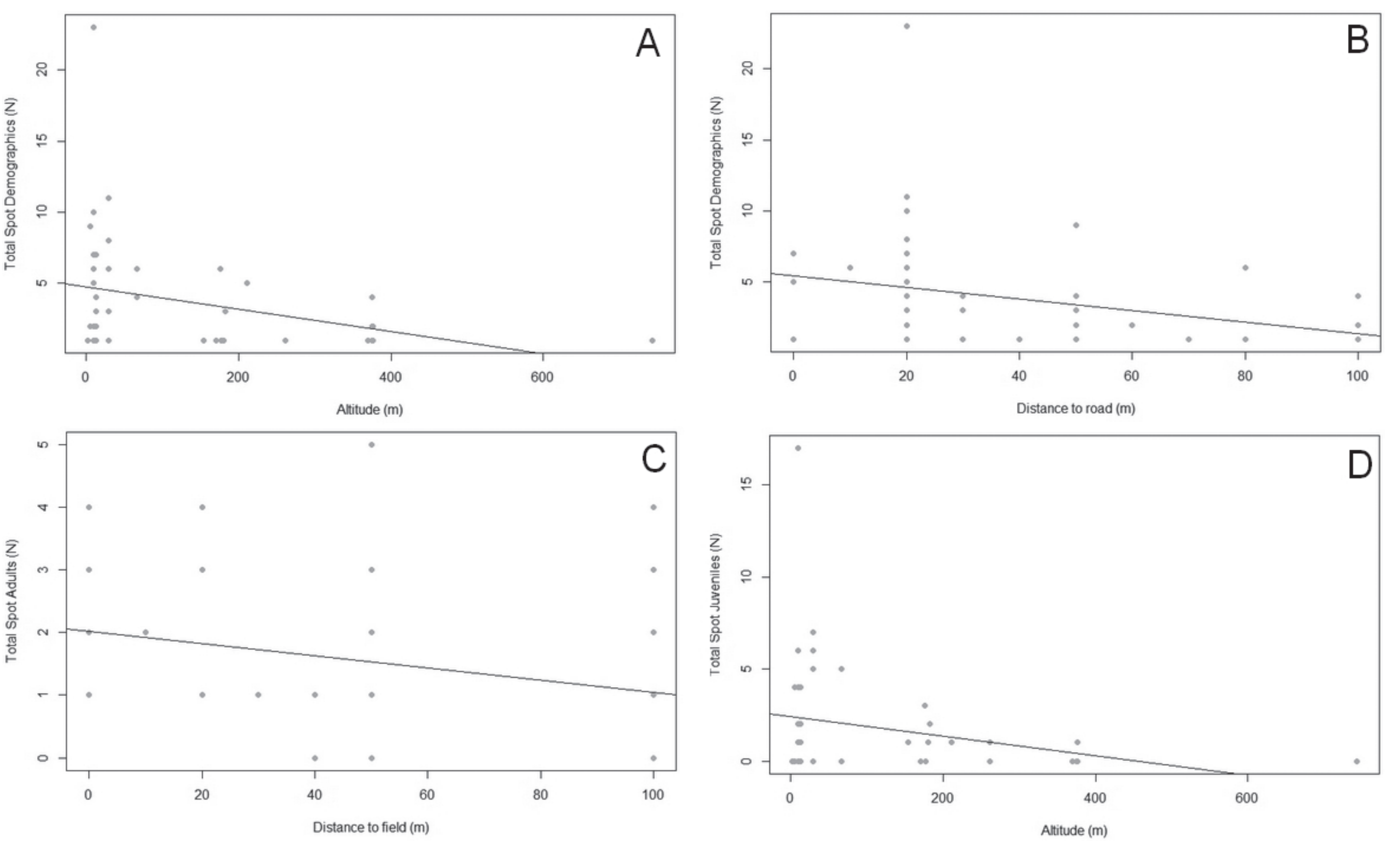

Fig. 3. Impact of anthropization factors on different demographics in *Clonistria guadeloupensis* in Guadeloupe. **A.** Effect of Altitude on Total Demographics ($P < 0.05$, see Table 1); **B.** Effect of distance to first Road on Total Demographics; **C.** Effect of distance to first Field on Adult Demographics; **D.** Effect of Altitude on Juvenile Demographics. The effects are marginally significant ($P < 0.10$) for graphs B, C and D (see Table 1) but illustrative of a general pattern for the species.

Conclusion

This study demonstrated a lack of strong human disturbance effect in niches of the stick insect *Clonistria guadeloupensis*, with a pattern of greater demographics for all stages in proximity to anthropized habitats, possibly associated with a greater openness of vegetation and easier dispersal. Describing occurrences of species over the human disturbance continuum is an important step in understanding how diversity may coexist with increased human occupancy. Increasing the number of studies focusing on the factors involved in adaptation to disturbance throughout the anthropization continuum, especially regarding dispersal and colonizing success, would allow finer prediction of the effect of further anthropization. Such research will also facilitate the determination of key factors for increasing the coexistence of humans and a putatively broader spectrum of species.

Data availability statement

Data are available on request from the corresponding author.

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