Leaf herbivory and fluctuating asymmetry as indicators of mangrove stress

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Abstract Fluctuating asymmetry (FA), a widely used measure of developmental instability in plants and animals, which describes random differences in size and/or shape between the two sides of a bilateral character. We used FA as a tool to detect stress in three mangrove species (*Avicennia germinans*, *Laguncularia racemosa*, *Rhizophora mangle*), growing in both disturbed and conserved habitats in the Atlantic coast of Mexico. In this region, disturbed habitats are the result of deforestation, livestock, tourism and agriculture activities. Twenty plants of each species were sampled in each of four sites (two disturbed and two conserved) and levels of FA, proportion of individuals with herbivory, proportion of leaves with damage, and leaf area removed by herbivores were evaluated. In disturbed habitats, regardless of plant species, more plants were attacked by insects, more leaves were damaged, and more leaf area was removed by herbivores, indicating higher overall damage to plants. We detected that FA levels varied significantly

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amongst mangrove species, they were higher in disturbed compared to conserved habitats, indicating the importance of FA as a monitoring tool of mangrove stress. A positive relationship between FA and herbivory levels also indicates that herbivores might be a source of stress.

Introduction

Plants have to constantly deal with a suite of abiotic and biotic stressing factors such as available nitrogen and water deficit, herbivory and pathogen incidence (Suzuki et al. 2014), which might infer into different physiological costs (Heil and Bostock 2002). Despite that plants have molecular, physiological, and cellular modifications to adapt to stressful events (Heil and Bostock 2002; Rozendaal et al. 2006), in some instances they are unable to perform regulatory processes, which can result in developmental instability of different organs (Escós 1997). Developmental instability is the inability of a genotype to consistently produce the same phenotype in a particular environment, and it has been suggested as an indicator of environmental and/or genetic stress (Møller and Swaddle 1997). Fluctuating asymmetry (FA) is a widely used measure of developmental instability in plants and animals. It describes the random differences in size and/or shape between the two sides of a bilateral character (Palmer and Strobeck 1986; Møller and Shykoff 1999). Individuals that develop in a stress-free environment are capable of buffering most of the random errors in their development (Freeman et al. 2005), but as environmental stress increases, the resilience of such organisms to recover from disturbances decreases, resulting in higher FA (Leamy and Klingenberg 2005; Cuevas-Reyes et al. 2013). FA is therefore predicted to increase in organisms that experience increased levels of environmental stress and is often considered an integral component of individual fitness, revealing perturbations of genetic or environmental origins (Leamy and Klingenberg 2005; Cuevas-Reyes et al. 2011a).

Fluctuating asymmetry in plants can be influenced by abiotic factors such as pollution, altitude,

temperature and soil fertility (Cornelissen et al. 2003; Freeman et al. 2004; Beasley et al. 2013), as well as biotic factors such as hybridization, parasitism and herbivory (Freeman et al. 2004; Albarrán-Lara et al. 2010; Cuevas-Reyes et al. 2011a, b, 2018). Particularly, the relationship between FA and herbivore susceptibility is still ambiguous. In some cases, leaf FA is positively related with the levels of herbivory (Cornelissen and Stiling 2005; Cuevas-Reyes et al. 2011a, 2018), but in other cases, no relationship has been found (Telhado et al. 2010). In the same way, several studies have documented the effects of habitat disturbance on leaf FA in plants of different terrestrial ecosystems such as tropical and temperate forests (Freeman et al. 2004; Nagamitsu et al. 2004; Beasley et al. 2013), but little information is yet available for plant species of coastal areas and estuaries (but see Torrez-Terzo and Pagliosa 2007; Constantino et al. 2009).

Mangroves are one of the most productive ecosystems in the world. The high availability of nutrients from rivers and land runoffs, and their effective recycling through microbial mineralization, contribute to coastline protection (Bouillon et al. 2008; Nagelkerken et al. 2008). Mangroves are considered ''key-ecosystems'' because they provide a wide variety of environmental services and denote habitat, shelter and food for numerous organisms (Mumby et al. 2004; Nagelkerken et al. 2008). However, it is also one of the most seriously threatened environments with global losses exceeding 35% as a result of human activities that are related to land use conversion of mangroves to mariculture, agriculture, forestry, urbanization, oil exploration and tourism (Campagna et al. 2011; Valiela et al. 2001). Particularly, in Mexico, the main threats to mangroves are habitat destruction, pollution and over-exploitation of resources. The lack of urban, industrial and tourist development planning, as well as agricultural, livestock and aquaculture development, have displaced and reduced considerable extensions of mangroves (CONABIO 2009). Finally, another source of mangrove disturbance are the urban solid waste, industrial pollutants, pesticides and agricultural fertilizers, which have had a great negative impact on mangroves communities.

Herbivory is one of the most important biotic interactions that affects the functioning of mangrove ecosystems (Elster et al. 1999). Specifically, leaf chewers (i.e. folivores), including crabs, birds and

insect species, have high leaf consumption rates of mangrove leaves (Feller 1995; Kathiresan 2003). The general pattern of herbivory by this insect guild in the mangrove species shows a range of 0.3% to 35% of the leaf area consumed. However, these values of leaf consumption are highly variable between species, individuals and/or sites (Robertson et al. 1992). For example, the levels of herbivory in *Rhizophora mangle* varies from 4 to 25%, while in *Avicennia germinans* are from 8 to 36% (Farnsworth and Ellison 1991). According to some authors, leaf chewers require consuming a great amount of mangrove leaves, since they generally have low nutritional quality and therefore, represent a poor source for this insect guild (Feller 1995; Kathiresan 2003).

The high rates of herbivory can cause lethal injuries to mangrove trees (Kathiresan and Bingham 2001), but there is a lack of information regarding data on FA as a monitoring tool of mangrove stress and their potential relationship with the herbivory patterns. Therefore, we used a multi-species approach to determine herbivory susceptibility in three mangroves species and the importance of fluctuating asymmetry as an indicator of environmental stress in disturbed habitats in Mexico. We addressed the following questions: (1) Do herbivory levels differ between mangrove species? (2) Are mangrove species more susceptible to herbivory in disturbed compared to conserved habitats? (3) Are levels of leaf FA affected by habitat disturbance in mangrove species? (4) Do FA patterns correlate with the levels of herbivory? We hypothesize that in disturbed habitats, mangroves will be more stressed and will have higher levels of leaf FA, and accordingly higher herbivory susceptibility.

Materials and methods

Study site

This study was conducted in the northwest limit of La Mancha Lagoon in the state of Veracruz, Atlantic coast of Mexico (96°22′W, 19°35′N). The climate is warm, sub-humid with a cyclone influence; the mean annual precipitation is 1234 mm. In this area, *Laguncularia racemosa* (L.) Gaertn F. (Combretaceae), *Rhizophora mangle* (L.) Linnaeus (Rhizophoraceae) and *Avicennia germinans* (L.) Linnaeus (Acanthaceae) occur in sympatric conditions along a mosaic

of conserved and disturbed habitats as result of deforestation, livestock, tourism and agriculture activities. These mangrove species are used in Mexico for local housing construction, fences, poles to catch fish, tool handles, carpentry, telegraph poles, electrical wiring, railroad ties, framed in boats, as well as for fuel (Utrera-López and Moreno-Casasola 2008).

Study system

Laguncularia racemosa (white mangrove): is a common component of mangrove forests along the Pacific and Atlantic coasts of Mexico (Rzedowski 1978). It is a perennial tree that can reach 10 m in height and occupies the medium to high intertidal zone of mangrove forests and colonizes disturbed sites, where it can form pure stands (Tomlinson 1986; Sobrado 2005).

Avicennia germinans (black mangrove): it occurs in most mangroves of the Atlantic and the Pacific coasts. It is a perennial shrub, usually 2 to 8 m high, characteristic of flooded areas of salt or brackish water.

Rhizophora mangle (red mangrove): is an evergreen tree or shrub, from 1.5 to 15 m (up to 30 m). This species has a broad distribution in Mexico and occurs along of the Gulf Coast, the Pacific and the Caribbean, in such extreme latitudes as Isla San Esteban in Baja California. This species is distributed on the Gulf side, from Tamaulipas to Veracruz, Yucatan and Quintana Roo. At the Pacific coast from Baja California to Sonora and Chiapas. These mangrove species have an associated herbivore fauna that includes dipteran and lepidopteran larvae, mites, hemipterans, crabs and even birds (Piyakarnchana 1981; Kathiresan 2003). We did not identify the herbivores that cause leaf damage in our mangrove species studied. Therefore, we only quantified the total herbivory, independently of the causative agent.

Data sampling

The central coast of the Gulf of Mexico has a considerable proportion of wetlands (3.8%) (Calles et al. 1998). Particularly, two-thirds of the wetlands in Veracruz are freshwater, and most of them are found in the coastal plain. Historically, these lands of the Gulf of Mexico have been used intensively for agriculture (corn crops) during the last thousand years,

and currently around 70% of the territory has been transformed into pastures for cattle ranching and agricultural fields of sugarcane (Doolittle 1987; Moreno-Casasola et al. 2009).

To examine the differences in leaf area consumed by herbivores and FA levels, we selected two intact areas "conserved" and two disturbed areas where *R. mangle*, *L. racemose*, and *A. germinans* occur in La Mancha Lagoon, Mexico. The conserved areas are located within a private reserve of conservation of the Institute of Ecology A.C., where there are no human activities and the mangrove species represent a closed canopy belt near the banks of the lagoon system. The disturbed areas occur outside of the reserve and are characterized by the presence of human activities such as livestock, fishing, logging and even urbanization. Some studies indicate that these conserved habitats have mean interstitial salinity ranging from 27.0 to 32.5 ppt, and annual leaf litter production ranging between 6.92 t/ha/year and 13.5 t/ha/year (Utrera-López and Moreno-Casasola 2008; Moreno-Casasola et al. 2009). In our knowledge, there is no data of physicochemical parameters of mangrove communities in disturbed habitats that occur outside of the reserve La Mancha, Veracruz. However, in both habitat conditions, a continuous flood occurs and the sediment is inundated during at least six to eight continuous months per year, mainly during the dry season (from October to April) (Moreno-Casasola et al. 2009).

We randomly selected 20 individuals of each mangrove species at each study site. From each individual, we randomly collected 50 fully expanded mature leaves, sampling on superior, intermediate and inferior canopy strata (Cuevas-Reyes et al. 2011a, b).

Fluctuating asymmetry measurements

Fluctuating asymmetry was calculated in 25 fully expanded intact mature leaves of each individual. A digital image was obtained for each leaf. We measured the distance from the right side (Rw) and left side (Lw), from the leaf edge to the midrib at the midpoint of the leaf corresponding to its widest part. Fluctuating asymmetry was calculated as the absolute value of the difference between the distances from the midrib to the left and right margins of the leaf ($|Ai − Bi|$), divided by the average distance ($Ai + Bi/2$), to correct for the fact that asymmetry may be size-dependent

(Cornelissen and Stiling 2005; Cuevas-Reyes et al. 2011a, 2018). Additionally, 10 leaves were blindly re-measured, without reference to previous measurements to control the measurement error in FA. We then evaluated the degree of significance of FA relative to measurement error using a two-way mixed-model ANOVA. The significance of the interaction (individual × leaf × side) indicated that variation in FA was greater than expected by measurements error ($F_{9, 25} = 33.9$; $P < 0.0001$).

According to Palmer and Strobeck (1986), there are three types of asymmetry, each characterized by a different combination of mean and variance of the distribution of right-minus-left (R−L) differences. Fluctuating asymmetry is found when the R-minus-L differences are normally distributed with a mean value of zero. Directional asymmetry is found when the R-minus-L differences are also normally distributed, but with a mean that is significantly different from zero. Antisymmetry is characterized by a platykurtic or bimodal distribution of R-minus-L differences about a mean of zero. To determine whether our data fitted only FA and no other types of asymmetry, we performed a Student's t test and Lilliefors' normality test to test whether mean values of signed right-minus-left values differed significantly from zero (Telhado et al. 2010; Alves-Silva and Del-Claro 2016). We found that R-minus-L measurements did not differ from zero ($t = 1.1$; $P > 0.05$), and therefore, we discarded the presence of directional asymmetry in our data. In the same way, we also rejected the presence of antisymmetry because our data (R-minus-L) exhibited a normal distribution ($P > 0.05$).

Herbivory levels

The herbivory levels were estimated in 25 leaves selected randomly per individual plant. We took a digital image of each leaf to calculate the total leaf area and the area removed by herbivores, using the Image analysis software for plant disease quantification (Assess Image). The proportion of leaf area removed by herbivores was calculated for each leaf by dividing the leaf area consumed by the total leaf area. To control for plant size, we measured plant height and diameter at breast height (DBH) (Cuevas-Reyes et al. 2013).

Statistical analyses

A generalized linear model applying the GENMOD procedure was performed to evaluate the frequency of leaves damaged by herbivorous insects in each habitat condition. The model used mangrove species as independent variables. The number of leaves with herbivory divided by the total number of leaves was used as the dependent variable. We used a Poisson error distribution and a Logit link function (SAS 2000; Stokes et al. 2000).

We performed a two-way ANOVA to compare herbivory levels amongst the three plant species in each habitat condition. Mangrove species and habitat condition were considered as independent variables and mean leaf area removed by herbivores used as the response variable in each case. An LSMeans test was performed as post hoc comparison ($P < 0.05$).

The differences in FA between the three-mangrove species in each habitat condition were evaluated using a logistic regression analysis, using GENMOD (SAS 2000; Stokes et al. 2000). The model considers mangrove species and habitat condition as independent variables. FA was used as response variable (SAS 2000; Stokes et al. 2000). Finally, we used Spearman's rank correlation analysis to determine the relationship between FA, herbivory, total leaf area, plant height and DBH, for each mangrove species in each habitat condition. Since these tests involved multiple comparisons, a Bonferroni correction was applied to adjust p-values.

Results

We found higher herbivory levels in disturbed habitats for all mangrove species (Table 1). Particularly, *R. mangle* was the species with higher proportion of leaves damaged (85.4% ± 3.3%) in comparison with *L. racemosa* (77.3% ± 2.1%) and *A. germinans* (67% ± 3.5%). Conversely, we found in conserved habitats that the proportion of damaged leaves was lower than undamaged leaves in the three-mangrove species (Table 1). The average percentage of leaves with damage in *A. germinans* was 29.5.3% ± 2.8%, in *R. mangle* was 22.3% ± 1.8% and in *L. racemosa* was 20.3% ± 1.8%.

Leaf area removed by herbivores was different between mangroves species (Table 1). The leaf area

Table 1 Effects of habitat condition (disturbed and conserved) and mangrove species on herbivory and fluctuating asymmetry

Effects	d.f.	F/χ^2	$P <$
Frequency of leaf damage			
Plant species (disturbed)	2	28.1	0.001
Plant species (conserved)	2	32.1	0.001
Leaf area removed			
Habitat condition	1	123.1	0.0001
Plant species	2	56.8	0.001
Fluctuating asymmetry			
Habitat condition	1	129.3	0.001
Plant species	2	79.5	0.001

removed was higher in *R. mangle* (8.7% ± 0.23) followed by *L. racemosa* (5.7% ± 0.18) and *A. germinans* (3.8% ± 0.35). In addition, the leaf area removed by herbivores was higher in disturbed than in conserved habitats in the three-mangrove species (Table 1).

The results of the analysis using the GENMOD procedure indicated that fluctuating asymmetry levels differed between mangrove species according to the logistic regression analysis (Table 1). In addition, FA was higher in disturbed (0.17 ± 0.03) than in conserved (0.04 ± 0.005) habitats (Table 1). In the case of *L. racemosa*, after a Bonferroni correction, Spearman's rank correlation showed that leaf area removed was negatively correlated with the total leaf area, whereas total leaf area showed a positive relationship with plant height and DBH in conserved habitats (Table 2a). In disturbed habitats, we found a positive relationship between FA and leaf area removed, total leaf area, plant height and DBH (Table 2a). In *R. mangle*, under conserved habitat conditions, a similar set of relationships was found, as leaf area removed was negatively correlated with the total leaf area, while positive relationships were found between total leaf area and DBH, plant height and DBH (Table 2b). In disturbed habitats, FA and leaf area removed, plant height, total leaf area and DBH, were positively correlated (Table 2b). A positive relationship was found between plant height and DBH in *A. germinans* under conserved habitat conditions, while in disturbed habitats, positive relationships were found between

Table 2 Spearman's correlation coefficients of plant traits, herbivory and fluctuating asymmetry. *Laguncularia racemosa* (a); *Rhizophora mangle* (b) and *Avicennia germinans* (c) in conserved and disturbed habitats

	Leaf area removed	Fluctuating asymmetry	Total leaf area	Plant height	DBH	
(a)						
Leaf area removed	–	0.11	− 0.34**	0.08	0.13	**Conserved**
Fluctuating asymmetry	0.94**	–	0.06	0.05	0.08	
Total leaf area	0.17	0.04	–	0.51**	0.45**	
Plant height	0.11	0.16	0.45**	–	0.54**	
DBH	0.15	0.12	0.66**	0.71**	–	
Disturbed						
(b)						
Leaf area removed	–	0.18	− 0.44**	0.08	0.08	**Conserved**
Fluctuating asymmetry	0.71**	–	0.12	0.05	0.04	
Total leaf area	0.12	0.11	–	0.11	0.35**	
Plant height	0.19	0.14	0.49**	–	0.38**	
DBH	0.23	0.08	0.78**	0.56**	–	
Disturbed						
(c)						
Leaf area removed	–	0.11	0.14	0.12	0.12	**Conserved**
Fluctuating asymmetry	0.73**	–	0.08	0.09	0.09	
Total leaf area	0.22	0.08	–	0.08	0.13	
Plant height	0.15	0.17	0.65**	–	0.48**	
DBH	0.13	0.11	0.58**	0.62**	–	
Disturbed						

** Significant values ($P < 0.05$)

FA and leaf area removed, plant height, total leaf area and DBH (Table 2c).

Discussion

Mangroves have been perceived as a highly resilient ecosystem to disturbance, as they have specific adaptations that allow them to resist natural disasters such as a tsunami or climatic changes (Lugo 1980; Alongi 2002). However, some studies have demonstrated that under disturbance conditions such as urbanization, industrialization, pollution (i.e. heavy metal presence), the levels of environmental stress increase in some species of mangroves (Alongi 2002; Feng-Qin et al. 2007). In our study, we demonstrated that individuals of *R. mangle*, *L. racemosa* and *A. germinans* exhibited significantly higher levels of fluctuating asymmetry in disturbed than in conserved habitats, corroborating our hypothesis that mangrove species experience higher levels of environmental stress in disturbed habitats, and therefore, have higher levels of FA (Møller and Swaddle 1997; Lens et al. 2000; Cuevas-Reyes et al. 2011a, 2018).

Habitat disturbance affects species composition, abundance and distribution of herbivores in different ways, increasing resources for some herbivorous or reducing resources for others (Barberena-Arias and Aide 2002; Cuevas-Reyes et al. 2018). Herbivore abundance and herbivory levels may be reduced, as a result of changes in environmental conditions, plant nutritional quality and/or concentration of defensive compounds of plants (bottom-up effects) (Cuevas-Reyes et al. 2013; Maldonado-López et al. 2015). For example, high temperatures and deficiency of water availability, which is characteristic of disturbed habitats, may accelerate different biochemical processes that alter herbivore growth and development, resulting in the reduction of body size and alterations in their life history and patterns of reproduction (Angilletta 2009; Lee and Roh 2010). Conversely, habitat disturbance might cause increased insect abundance and

herbivore damage through top-down effects, when population decline of higher trophic levels such as parasitoids and natural enemies positively affect herbivore density and herbivory levels (Arnold and Asquit 2002; Tscharntke et al. 2007). For oak forests, Maldonado-López et al. (2016) showed that both plant quality (leaf, bud and petiole production) and herbivory by insects were higher in isolated plants and smaller forest fragments in comparison with larger fragments of oak forests. Our findings for the mangroves are in accordance with this idea considering that plants can be influenced by the changes in abiotic conditions associated with habitat disturbance such as increased temperature, salinity and irradiation, which in turn, indirectly affect the interactions between mangrove species and their herbivorous insects via "bottom-up effects" (i.e. changes in plant nutritional quality and/or concentration of defensive compounds of plants) (Cuevas-Reyes et al. 2013; Maldonado-López et al. 2015), increasing the proportion of damaged leaves by herbivores. In addition, leaf area removed by insects was higher in disturbed than in conserved habitats for all mangrove species evaluated. Because FA has been considered as an indicator of environmental stress in different groups such as birds, mammals, fishes, amphibians insects, humans and plants (Wauters et al. 1996; Blackenhorn et al. 1998; Allenbach et al. 1999; Hansen et al. 1999; Møller and Shykoff 1999; Rikowski and Grammer 1999; Anciles and Marini 2000; Söderman et al. 2007; Cuevas-Reyes et al. 2011a, b, 2013), we propose that higher levels of fluctuating asymmetry recorded in mangrove species in disturbed habitats, suggest more environmental stress and therefore, more susceptibility to insect herbivore attack in this habitat conditions.

Our results can be explained by "The Plant Stress Hypothesis" (White 1984; Mattson and Haack 1987) that states that environmental stress negatively affect plant resistance to herbivory by altering biochemical source-sink relationships and the chemical composition of leaves, leading to a more attractive and palatable food to herbivores (Rhoades 1983; Mattson and Haack 1987; Cornelissen and Stiling 2005). The mechanism that support this hypothesis is that plants under stress conditions increase the levels of amino acids and decrease the production of secondary metabolites (such as tannins and phenols) in their tissues, which in turn, increase insect performance, the opportunity of offspring survival and susceptibility to herbivory (Torrez-Terzo and Pagliosa 2007).

We found differences in the herbivory levels between mangrove species, A. germinans had the lowest level of leaf area consumed, followed by L. racemosa and R. mangle. Differences in plant chemistry, leaf palatability, local microclimate have been suggested as possible causes for these differences (Joern and Mole 2005; Bauerfeind and Fischer 2013). Particularly, mangrove species can survive in stressful environments with hypersaline conditions, due to evolution of physiological and anatomical mechanisms to conserve water and eliminate salts, as is the case mainly of A. germinans, and to a lesser extent in L. racemosa and R. mangle (Sobrado 2005; Parida and Jha 2010). As a consequence, these plant species have variation in the levels of leaf sclerophilly (Feller 1995; Gonçalves-Alvim and Fernandes 2001), which are characterized by having a low nutritional quality, higher concentrations of chemical compounds, great thickness and hardness that in turn, reduce the probability of abscission and the herbivore incidence (De lacerda et al. 1985; Fernandes and Price 1988; Tavares de Menezes and Peixoto 2009). Therefore, it is possible expected that the levels of damage caused by herbivores of free-living such as leaf chewers decrease in plant species with scleromorphic leaves in comparison with others herbivory guilds such as gall-inducing insects and leaf miners (Price et al. 1998; Feller 2002).

A positive relationship between foliar FA and leaf area removed by herbivores was found only in disturbed habitats for the three-mangrove species evaluated. Because habitat disturbances change some environmental conditions (i.e. air quality, soil fertility, temperature and humidity) that may affect not only the patterns of plant growth but also plant responses to herbivory, increasing nutritional quality and/or decreasing secondary chemistry compounds production (Cornelissen and Stiling 2011), resulting in greater susceptibility to herbivory (Cornelissen and Stiling 2005; Lempa et al. 2000). In particular, human activities such as logging, fishing, livestock and urbanization have strong impacts on mangrove communities through their effect on abiotic factors and biodiversity. In particular, it has been shown that mangrove disturbances affect fluvial sedimentation patterns by increasing pollution by hydrocarbons, organochlorine pesticides and other chemical

compounds produced by agricultural effluents (Lewis et al. 2011). In addition, mangrove disturbance affect different soil biochemical parameters, decreasing microbial biomass C, microbial biomass N, N flush, basal respiration, metabolic ratio (qCO2), ATP N mineralization rates and dehydrogenase and catalase activities (Dinesh et al. 2004). Finally, logging of mangrove forests results in an increase of CO_2 emissions due to the oxidation of carbon in mangrove peat. This additional oxidation can occur if peat is disturbed and air contact increases, as would be the case when shrimp ponds are built on peat soils and peat is pushed into banks or dams (Lovelock et al. 2011). These abiotic changes in mangroves communities as result of disturbances can affect de ecology and therefore, the antagonistic interactions of mangroves species. Our results suggest that habitat disturbance causes a reduction of habitat suitability for *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia germinans*, which is expressed in higher foliar FA levels, influencing nutritional quality and/or defensive chemical compounds making them more susceptible to herbivore incidence (Cuevas-Reyes et al. 2013). Finally, our results highlight the importance of FA as a valuable biomarker for habitat disturbance and provides a quick, cheap and valuable cue to evaluate the early stages of environmental disturbance (Torrez-Terzo and Pagliosa 2007) and its effects on the dynamics of plant–insect interactions through herbivory.

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