



## Original article

## Describing a multitrophic plant-herbivore-parasitoid system at four spatial scales

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## ARTICLE INFO

## Article history:

Received 2 August 2013

Accepted 21 October 2013

Available online 13 November 2013

## Keywords:

Mexico

Multitrophic

*Ruellia nudiflora*

Spatial scale

*Tripudia quadrifera*

Yucatan

## ABSTRACT

Herbivore-parasitoid interactions must be studied using a multitrophic and multispecies approach. The strength and direction of multiple effects through trophic levels may change across spatial scales. In this work, we use the herbaceous plant *Ruellia nudiflora*, its moth herbivore *Tripudia quadrifera*, and several parasitoid morphospecies that feed on the herbivore to answer the following questions: Do herbivore and parasitoid attack levels vary depending on the spatial scale considered? With which plant characteristics are the parasitoid and the herbivore associated? Do parasitoid morphospecies vary in the magnitude of their positive indirect effect on plant reproduction? We evaluated three approximations of herbivore and parasitoid abundance (raw numbers, ratios, and attack rates) at four spatial scales: regional (three different regions which differ in terms of abiotic and biotic characteristics); population (i.e. four populations within each region); patch (four 1 m<sup>2</sup> plots in each population); and plant level (using a number of plant characteristics). Finally, we determined whether parasitoids have a positive indirect effect on plant reproductive success (seed number). Herbivore and parasitoid numbers differed at three of the spatial scales considered. However, herbivore/fruit ratio and attack rates did not differ at the population level. Parasitoid/host ratio and attack rates did not differ at any scale, although there was a tendency of a higher attack in one region. At the plant level, herbivore and parasitoid abundances were related to different plant traits, varying the importance and the direction (positive or negative) of those traits. In addition, only one parasitoid species (*Bracon* sp.) had a positive effect on plant fitness saving up to 20% of the seeds in a fruit. These results underline the importance of knowing the scales that are relevant to organisms at different trophic levels and distinguish between the specific effects of species.

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## 1. Introduction

The study of herbivore-parasitoid interactions must be conducted using a multitrophic and multispecies approach. The relevance of this approach has been largely recognized since Price et al. (1980) claimed that the study of plant–insect interactions must consider the third trophic level. Consequently, numerous studies have reported different types of direct and indirect top–down (Gómez and Zamora, 1994; Rudgers, 2004) and bottom-up effects (Gols and Harvey, 2009; Hilker and Meiners, 2002; but see Van der Meijden and Klinkhamer, 2000) stating the importance of a multitrophic approach.

Spatial scales have been proven to change the relation between biotic and abiotic variables. For this reason, it is fundamental to find the relevant scales to which organisms respond (Kotliar and Wiens, 1990). In plant-herbivore-parasitoid tri-trophic interactions, there has been an increasing interest to know how each trophic level responds to landscape complexity (Von Zeipel et al., 2006; Gagic et al., 2011) and/or scale (Thies et al., 2003; Cogni and Futuyama, 2009; Rusch et al., 2011; Tschardt et al., 2007; Abdala-Roberts et al., 2010). These works have found that herbivores and parasites respond to landscape complexity (i.e. habitat diversity, connectivity, crop-noncrop area, etc.), but that this response depends on the scale area considered.

On a smaller scale (e.g. within patch), different types of visual, olfactory and mechanic plant-level cues have been studied (e.g. Prokopy, 1983; Vet and Dicke, 1992; Cloyd and Sadof, 2000; Hilker and Meiners, 2002; Völkl, 2000). These cues influence herbivore and parasitoid behaviors. One general assumption is that parasitoids use cues in a hierarchical manner according to the relative importance of such cues at each spatial scale (Fischer

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et al., 2001; Jarošík and Lapchin, 2001). For example, cues such as plant size can be used by herbivores to detect suitable plants at distances of several meters, while color among plant parts can be used as a foraging cue (Prokopy, 1983). In the case of parasitoids, synomones can be detected from long distances (Vet and Dicke, 1992), while visual cues can be useful at a few meters distance, and mechanical cues can be used at shorter distances (Fischer et al., 2001; Völkl, 2000). The importance of these cues at each spatial scale becomes more complex when considering a multitrophic approach.

We studied the multitrophic system composed of the herbaceous plant *Ruellia nudiflora* (Engelm. and Gray) Urban (Acanthaceae), its herbivore a predispersal seed-predator *Tripudia quadrifera* (Zeller) (Lepidoptera: Noctuidae), and several parasitoid species which attack the herbivore. We asked the following questions: Do herbivore and parasitoid attack levels vary depending on the spatial scale considered (region, population and patch)? With which plant traits, at the plant level, are the parasitoid and the herbivore associated? Do parasitoid species vary in the magnitude of their positive indirect effect on plant reproduction? To address this, we look at herbivore and parasitoid abundances on the plant *R. nudiflora* at four spatial scales in the Yucatan Peninsula (Mexico). We assume that the scales at which the abundances vary indicate the scale at which herbivores and parasitoids found heterogeneity in their environment (in the sense of Kotliar and Wiens, 1990). Here, we consider spatial scale as the size of the area in which the plants can be immersed and we discuss the factors that could drive those responses: plant individuality (plant characteristics), patch level (close surroundings), population (local environment), and region (regional climate).

## 2. Materials and methods

### 2.1. Study species

*R. nudiflora* (Engelm. and Gray) Urban, (Acanthaceae) is a self-compatible perennial herb, which typically measures 20–30 cm in height, and is found in land areas from Texas to SE Mexico. It grows mostly in disturbed open habitats and has a wide distribution across the state of Yucatan (Mexico). It has a long reproductive season (April–October) and has a mixed reproductive system as it produces both open flowers (chasmogamous) and flowers that remain closed (cleistogamous). It self-pollinates obligatorily and regardless of environmental conditions, cleistogamous flowers are produced first (Munguía-Rosas et al., 2013). Fruits are dry and dehiscent; each one normally bearing 10–12 seeds (Abdala-Roberts et al., 2010). Populations of *R. nudiflora* form dense patches which cover areas from 1 m<sup>2</sup> to 9 m<sup>2</sup> (M. Cuautle per. obs.).

Fruits are attacked by *T. quadrifera* (Zeller) larvae (Lepidoptera: Noctuidae), which feed on seeds prior to their dispersal. *T. quadrifera* is considered a species complex that contains six species (Pogue, 2009). The genus is confined to the New World where it occurs in the southern, Midwestern, and eastern United States, Mexico, the Caribbean, Central America, and South America. *T. quadrifera* represents the only recorded seed predator of *R. nudiflora* in the Yucatan Peninsula (Abdala-Roberts et al., 2010), and *Ruellia* genera is the only reported host plant for the *T. quadrifera* species complex (Pogue, 2009). Adult female moths oviposit on recently formed fruits, and the larva grows inside the developing fruit and usually consumes all its seeds. Before pupating, each larva excavates a tunnel which the adult uses to exit the fruit (Abdala-Roberts et al., 2010). Typically, only one larva is found per fruit, and several parasitoid species use the *T. quadrifera* herbivore as a host.

### 2.2. Sampling: region and population level

The field survey was conducted from 14 Jun 2006 to 27 Jul 2006, during the peak of the flowering and seed production season of *R. nudiflora*. The study was conducted in the state of Yucatan (SE Mexico), in three different regions (namely the north, center and south of the state) which strongly differ in terms of abiotic (temperature and rainfall) and biotic (type of forest) characteristics despite geographical proximity in some cases (see Abdala-Roberts et al., 2010). Specifically, there is a precipitation and temperature gradient from the north (drier and cooler) to the south (moister and warmer) (Abdala-Roberts et al., 2010). Thorny deciduous tropical forests are present in the northern region and deciduous and semi-evergreen tropical forests can be found in the central and southern regions, respectively (Abdala-Roberts et al., 2010). Soil conditions also vary; the northern region is characterized by a higher percentage of organic matter than the central region (Ortegón-Campos et al., 2012). A total of four *R. nudiflora* populations were sampled per region, and distances between populations within each region ranged from 2 to 70 km. All sampled populations were found in open disturbed areas next to tropical dry forest fragments.

### 2.3. Sampling: patch and plant level

Four 1 m<sup>-2</sup> plots (i.e. patch) were established within each of the four populations located in the north and south. In the central region there was just one plot of 4 m<sup>-2</sup> for each population (for this reason the patch analysis was restricted to the north and south). Within a given population, distance between patches was at least 5 m. Within each patch the number of *R. nudiflora* individuals was recorded, and for each plant we recorded: distance (cm) to closest plant, height, number of branches (as surrogates of size), number of flowers, floral buds, total number of fruits and total number of mature fruits. Mature fruits were collected and transported to the laboratory for their dissection and to record herbivore and parasitoid attacks.

### 2.4. Herbivore attack

Fruits collected ( $N = 1420$ ) in the field were transported to the laboratory where they were opened. For each fruit we recorded the following: number of viable (undamaged) seeds, number of seeds with signals of damage by the herbivore, and herbivore presence which was determined via direct (presence of larva) or indirect evidence (frass, escape tunnel).

### 2.5. Parasitoid attack

Parasitoid presence in fruits was determined by means of direct (presence of adult wasp) or indirect (empty cocoon or mummy) evidence. When only indirect evidence was available, parasitoids were assigned a morphospecies based on the type of cocoon. The morphospecies of parasitoids recognized were: *Bracon* sp. (Braconidae), Pteromalidae (corresponded to two morphospecies), Morphospecies 1 (it was not possible to identify any adult to parasitoid genera but it was possible to distinguish it from other parasitoids); a fly of the Tachinidae family, others (*Chelonus* sp., *Microchelonus* sp. and an Ichneumonidae morphospecies), and finally, unidentified (when it was not possible to assess a morphospecies based on the mummy). Braconidae family is formed by idiobiont (prevent further development of the host after initial parasitization; Hawkins, 1994) ectoparasites that parasitize middle and late larva instars (Delfín-González and Burgos-Ruiz, 2000). Those of the Pteromalidae family are idiobiont gregarious ectoparasites that parasitize larvae and pupa (<http://www.faculty.ucr.edu/~legnerref/>

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