On the occurrence of a highly localized outbreak of a saturniid in lowland east Ecuador: a case study and literature review

Samantha Sutton, Sarah C. Pasquini, TodD Swanson and Walter P. Carson

ABSTRACT
For decades, outbreaks of insect herbivores in tropical forests were considered unusual or rare events primarily because of high plant diversity and the top-down impact of enemies. An alternative explanation is that these outbreaks are common but occur on sparsely distributed hosts high in the canopy and at scales of one or a few individual trees. Here, we report an outbreak of a saturniid in the genus Citioica Travassos & Noronha near the Amazon Basin of Ecuador on a single tree of Inga edulis Mart. The outbreak caused near complete defoliation (>90% leaf loss) and did not occur on nearby conspecifics. This is only the twenty-third documented case of a saturniid outbreak, of which more than 60% occurred in tropical habitats. This is the first report of an outbreak on a single tree. Members of the local indigenous communities are well aware of these Citioica outbreaks and collect these caterpillars for food whenever outbreaks are detected, suggesting that these isolated outbreaks are fairly common. Further research is required to explore the possibility that insect outbreaks in tropical forests may be more common than previously suspected but occur over very small spatial scales undetected high in the forest canopy.

Introduction
Insect outbreaks in tropical forests are thought to be uncommon, particularly when compared to temperate or boreal forests. Indeed, Elton [1] argued that insect populations in the tropics are kept from outbreaks because of both high plant diversity and abundant enemies [2,3]. Consequently, the study and documentation of tropical insect outbreaks have been neglected [4–6]. Here, we define an insect outbreak as a rather sudden spike in population density relative to background densities on longer temporal or larger spatial scales [e.g., 7,8]. In addition, outbreaks can also be quantified by the degree of host defoliation, which is usually severe [reviewed by 8].

Tropical insect outbreaks may be overlooked because they occur high in the forest canopy, occur on sparsely distributed hosts, or occur on a single host plant located within a high-density host patch [5,8–12]. Thus, outbreaks may be common, but go undocumented because they are widely scattered, highly localized, and unpredictable in space and time [5,6,10,12]. To better evaluate the frequency and occurrence of outbreaks, Dyer et al. [5] argued that outbreaks should be documented in the peer-reviewed literature with information on the identity of the herbivore, its abundance, its hosts, and geographic location. These accounts could then be used to better understand the ecology of outbreaks. Importantly, from a phytocentric view, repeated outbreaks that cause major defoliation over the life of a long-lived tree could reduce host survival and fecundity, which may then impact forest dynamics and diversity [4,5,13,14]. Indeed, as Strong et al. [15] pointed out, “the role of rare events such as outbreaks … cannot be ignored as a force structuring ecological communities just because they are rare”. Here, we document an outbreak of a Citioica sp. Travassos & Noronha (Saturniidae, Ceratocampinae) on a single mature individual of the ice cream bean tree (Inga edulis Mart.) near the Amazon Basin of Ecuador. In addition, we briefly review the literature on the worldwide occurrence of outbreaks of saturniids.

Natural history of our focal species
Our study occurred at Tiyu Yaku, Napo, Ecuador at the Andes and Amazon Field School, also known as Iyarina (0.9963° S, 77.8136° W). This field station occurs within lowland evergreen rainforest with a Köppen-Geiger climate designation of Af [equatorial rainforest, fully humid: minimum monthly mean temperature ≥ 18°C, mean precipitation of the driest month ≥ 60 mm; 16]. Inga edulis is in the Fabaceae within the subfamily Caesalpinioideae [17]. It is an early successional native tree species with high rates of photosynthesis and...
growth [18]. *I. edulis* is also a domesticated crop, and trees growing in and around agricultural settings may have slightly lower allelic diversity versus wild populations [19], which may make these individuals more prone to suffering outbreaks, though this has not been tested. Leaves of *Inga* spp. produce nectaries located on the leaf rachis. These nectaries are present in both young and mature *Inga* leaves, though only nectaries on young leaves actively produce nectar to attract ants as a defensive mutualism. In addition to this defensive mutualism, *Inga* leaves produce an array of secondary defensive compounds, with young leaves showing a higher investment in these secondary metabolites than older leaves [20,21].

The indigenous Kichwa people often plant *I. edulis* on the periphery of agricultural clearings or leave naturally occurring individuals in place because mature adult trees shade perennial crops, fix nitrogen, provide edible fruits, and produce timber [22–24]. Our focal tree likely colonized naturally due to its location on the edge of a precipice. The caterpillar (*Citioica* sp.) is called “tupuli kuru” (pin caterpillar) in the Kichwa dialect (T.D. Swanson, personal observation). Before the caterpillars pupate, locals gather them as a food source, typically roasting them over fires, or forming the caterpillars into patties and frying them (W.P. Carson, personal observation).

**Methods**

To conduct our literature review, we used Google Scholar and Biosis with key words saturniid outbreak, insect outbreak + saturniidae, saturniidae AND insect outbreak, insect outbreak AND tropical insect outbreak. We also conducted a more traditional search using several recent reviews as entry ways into the literature [4,5].

Caterpillars were counted visually with the aid of binoculars from the ground surrounding the single focal tree (see description below). A random sample of caterpillars (n = 20) were measured for length and width at midpoint using a ruler.

**Results and discussion**

Caterpillars numbering at least 1000–1200 individuals caused nearly complete defoliation of a single individual of *I. edulis* from 23 July to 27 July 2017 (Appendix 1). The caterpillars averaged 6.8 cm in length (range: 5.0–7.7; n = 20) and 0.78 cm in width (range: 0.6–1.0 cm; n = 20). The species we observed had aposematic coloration and non-urticating spines (Appendix 2). We observed oropendolas (*Psarocolius* sp.) feeding on the caterpillars, suggesting the caterpillars were not well defended by toxic chemicals. The occurrence of so many caterpillars on a single individual tree suggests that their sheer numbers may function to overwhelm enemies allowing at least some to survive to pupation.

Caterpillars were members of the genus *Citioica* (Samuel Jaffe, the Caterpillar Lab, Amherst, Massachusetts, USA, personal communication), but we were not able to identify the caterpillars to species (attempts at rearing failed). Saturniids from the Napo Province, Ecuador include *Citioica kaechi* Brechlin [25] and *Citioica homoea* Brechlin [26], making them candidate species. *Citioica guayensis* Brechlin & Meister is found in French Guiana and has similar coloration and spinal arrangement, but our species had less yellow [27]. Without comparable images of candidate caterpillars, species identification necessitates a DNA sample or rearing to the adult stage.

The outbreak was highly localized on a single mature *I. edulis* (39.2 cm DBH) and two individuals of *I. edulis* less than 100 meters away from our focal tree were devoid of caterpillars. We did not observe the caterpillars on any nearby heterospecifics. Five other *I. edulis* individuals, within three kilometers of the outbreak, were also devoid of saturniids. Anecdotal reports suggest that *I. edulis* can recover from heavy bouts of defoliation [22] and our focal individual appeared healthy with an intact canopy, devoid of caterpillars, one year after the outbreak in July 2018 and also in March of 2019.

This was only the 23rd documented case of a saturniid outbreak in the scientific literature (Table 1). Similar to the case study here, Allen [28], and Criddle [29] documented highly localized outbreaks of saturniids that were less than 20 ha and 1.2 ha in area respectively. Paredes et al. [30] documented severe defoliation of *I. edulis* in Ecuador by the saturniid *Eacles imperialis* over an area of just 125 ha. Such highly localized outbreaks may be [31,32] common but simply go unseen or unreported, particularly if they occur within large expanses of continuous forest. For example, Grogan [33] reported that an unidentified *Thysanoptera* caused complete defoliation over a 500-m² area of forest in Southeast Brazil. For saturniids, outbreaks were typically larger, sometimes covering areas of more than 200,000 ha (Table 1).

Species within a single genus (*Hylesia* spp.) accounted for about 20% of the outbreaks, about one quarter of the outbreaks occurred on plant species within the Fabaceae, and more than 60% were in tropical habitats. Species within the Fagaceae, particularly within the genus *Quercus*, were also vulnerable to outbreaks in temperate regions. Overall, it is unknown how often highly localized insect outbreaks occur across the landscape and the degree that they occur repeatedly on the same host individual. We suggest that these types of outbreaks are more common than previously suspected but are simply overlooked or
Table 1. Twenty-three studies of Saturniidae outbreaks within 13 insect genera including the one sampled in this study. Outbreaks occurred in tropical savannas, and temperate and tropical forests.

| Forest Type                      | Location                      | Saturniid          | Host Plant                            | Documentation                                                                 | Outbreak Size | References                                                                 |
|----------------------------------|-------------------------------|--------------------|---------------------------------------|-----------------------------------------------------------------------------|---------------|---------------------------------------------------------------------------|
| Tropical Savannah                | Limpopo Province, South Africa | Imbrasia belina    | Goliapheum mopane (Fabaceae)          | Estimated larval densities using shade netting bags                          | >200,000 ha    | De Swardt et al. 2018 [34]                                               |
| Semi-arid tropical savannah      | Limpopo Province, South Africa | Cimina forda       | Burkea africana (Fabaceae)            | Estimates of biomass consumption                                            | 800 ha        | Scholes and Walker 1993 [35]                                              |
| Semi-arid broadleaf savannah     | Louisiana and Mississippi, United States | Hemicela maha      | Quercus spp. (Fagaceae)               | Observational; Host plant preference                                         | Widespread regional defoliation | Martinat et al. 1997 [36]                                                 |
| Temperate Forest                 | Oregon, United States         | Colorada pandora   | Pinus ponderosa; Pinus contorta (Pinaceae) | Used tree rings for identification of outbreaks                              | >1,000 ha; >75 ha | Brown 1984 [37], Speer et al. 2001 [38]                                    |
| Oak-hickory broadleaf forest     | New York and New Hampshire, United States | Dyocampa rubicunda | Acer rubrum, Acer saccharum (Sapindaceae) | Observational                                                                   | <20 ha        | Allen 1976 [28]                                                           |
| Coniferous forest                | Belair Resort, Quebec, Canada  | Anisota            | Quercus macrocarpa (Fagaceae)         | Observational                                                                   | 1,000 ha      | Serrano and Fortz 2003 [40]                                                |
| Northern hardwoods               | Carman, Manitoba, Canada      | Anisota            | Quercus macrocarpa (Fagaceae)         | Observational                                                                   | 1.2 ha        | Serrano and Fortz 2003 [40]                                                |
| Oak-pine mixed forest            | Gainesville, Florida, United States | Anisota            | Quercus spp. (Fagaceae)               | Observational                                                                   | ~1,000 ha     | nosotros                                                                  |
| Southern hardwoods               | Patagonia, Argentina          | Ornismodes         | amphimone (Fagaceae)                  | Larval densities                                                                | Widespread regional defoliation | nosotros                                                                  |
| Broadleaf rainforest             | Parana, Brazil                | Drupha             | Araucaria angustifolia (Araucariaceae) | Observational; Behavioral observations                                         | ~50,000 ha     | widespread regional defoliation                                           |
| Moist semi-deciduous broadleaf   | Costa Rica, Mexico, French Guiana, Trinidad | Hylesia spp.       | Multiple species* (Multiple Families) | Larval densities                                                                | <10,000 ha; a few trees; ~50 trees; widespread regional defoliation | Carrillo-Sánchez et al. 2002 [44], Janzen 1984 [45], Jourdain et al. 2012 [46], Pescador 1993 [31], Pescador 1995 [32], Polar et al. 2010 [47], Paredes et al. 2011 [30] |
| Dry broadleaf forest; mangroves   | Guayas Province, Ecuador      | Estes imperialis   | Theobroma caico (Malvaceae)            | Larval densities                                                                | 125 ha        | Widespread regional defoliation; widespread regional defoliation         |
| Cacao plantation                 | Brazil                        | Syphaxinae         | Scholecolobus paralyba (Fabaceae)     | Pest of cultivated parica trees                                              | 700 ha        | Batista et al. 2013 [48]                                                  |
| Parica plantation                | Northeast India               | Criola             | Mangifera indica (Anacardiaceae)      | Pest of cultivated mango trees (Outbreaks are controlled by parasitoids)       | Widespread regional defoliation; a few hosts | Widespread regional defoliation; a few hosts |
Table 1. (Continued).

| Location          | Saturniid Host | Single tree |
|-------------------|----------------|-------------|
| Lowland Tiyu, Napo, Ecuador | *Chorocha sp.*  | *Acocora edulis* (Fabaceae) |

Saturniids were often not identified to species.

ignored because of their ephemeral occurrence, and sporadic, small-scale nature.

**Acknowledgments**

We thank John Wenzel, Michelle Spicer, and Tiffany Betras for comments on various drafts of the manuscript.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**ORCID**

Samantha Sutton http://orcid.org/0000-0002-1491-7763

Walter P. Carson http://orcid.org/0000-0001-7246-3790

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Appendix 1. The *Inga edulis* was nearly completely defoliated by the end of the five-day outbreak.

Appendix 2. A caterpillar from the outbreak (A) and the underside of one of the *Citioica* sp. from the outbreak (B).