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Review

Thrips in the Neotropics: What do we know so far?

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ABSTRACT

Thrips are among the most diverse insects in the planet, however their diversity and interactions in Neotropics are not well known. Most studies in this region regard the Brazilian and Argentine thysanopterofauna and treat species as crop pests either by the severe herbivory on plants and by the transmission of virus resulting in serious damage and economic losses. Nevertheless thrips present unique and extraordinary interactions and occur in virtually any microhabitat, such as flowers, leaves and fruits. These insects may feed on fungus, flower tissues and also on other arthropods, influencing food chains and bottom-up and top-down forces in trophic cascades. In addition to these widely disparate feeding habits, thrips exhibit a diverse array of life styles including various levels of sociality, remarkable structural polymorphisms, gall-induction on leaves and pollination as well as ectoparasitism and phoresy behavior in hemipteran species. Intertwined with this astonishingly broad range of niche occupation and life histories there is an inherent opportunism that allows many species to readily adopt and utilize a variety of resources in ephemeral and/or stable habitats. In this review we present a general overview of thrips ecology and biology and make available information on the current knowledge on thrips habits and habitats in the Neotropics. We also aim to shed light and provide an insightful assessment on the ecology and behavior of these long ignored insects in one of the most biologically diverse ecozones in the world.

KEYWORDS: Thysanoptera, diversity, ecology, interactions, tropical

Current knowledge of Thysanoptera in the Neotropics

Since the claims of Laurence Mound in the beginning of this century [1], pointing out that it was urgent and necessary the graduation of researchers interested on the study of Neotropical thrips, much progress was done. The main result was the great increase in the number of papers, directly related to thrips, published in journals worldwide. For instance, up to 1990 only a small bunch of articles were available dealing with thrips in Neotropics and the great part of them regarded taxonomy [2, 3, 4, 5, 6, 7] or thrips as crop pests [8, 9, 10]. Therefore whoever wished to venture to study Neotropical thrips in the last century faced the problem of the absence of basic information. With very few exceptions [11, 12, 13], researchers did not have a guide or technical knowledge for the study of thrips ecology and biology either in nature or in laboratory conditions.

Fortunately in the 21th century this situation began to change. We perceived it making an accurate bibliographic research on the three main known internet databases, in order to gather all

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information about the published papers about thrips in the last 20 years. This compilation of data enabled us to trace a profile of the current knowledge of thrips in different countries and compare the proportion of researches in temperate and tropical zones, as well as among the countries in the Neotropics. This survey was made on JStor (Journal Storage www.jstor.org), Scielo (Scientific Eletronic Library Online www.scielo.org), and ISI Web of Science (http://apps.isiknowledge.com/UA_GeneralSearch_input.do?product=UA&search_mode=GeneralSearch&SID=1CpNC3g4FijP8J789ED&preferencesSaved=) with the words “thrips” and “Thysanoptera” in search fields in JStor and Web of Science, and additionally the words “trips” and “tripes” in Scielo, the Spanish and Portuguese words for “thrips”, respectively. In Web of Science the research was refined in “articles”, “notes” and “countries”. We came across a total of 2182 documents from the three databases which were classified in respect to five thematic categories: 1) Pests: papers in which the subject was pest thrips in economic crops and in greenhouses and those that include the use of chemicals to suppress thrips populations; 2) Biological control: documents in which the objective was to test the value of arthropods feeding on thrips as biological agents and those which considered thrips themselves as biological control agents against weeds; 3) Taxonomy; 4) Biology: papers dealing with thrips behavior or studies on molecular biology; 5) Ecology: studies on thrips in natural areas, inventories, gall-making thrips, pollination, and population dynamics approaches.

The first results of this bibliographical analysis showed that in comparison to the 1990 decade the volume of papers with reference to thrips has increased considerably, comprising thrips occurrence in natural areas, feeding habits and interaction with other arthropods [14, 15, 16, 17]. Although much attention is still being focused on thrips as pests of economic crops, the life history of thrips in natural areas is coming out as a promising field (Figures 1 and 2).

Compared with Temperate zones, publications on Neotropical thrips were almost six times fewer, showing clearly that tropical species deserve further attention of biologists, ecologists, taxonomists and agronomists (Figure 3A). Furthermore, this investigation revealed that the most known and studied thrips fauna on Earth is that of the United States (Figure 3B). It is not only a direct result of

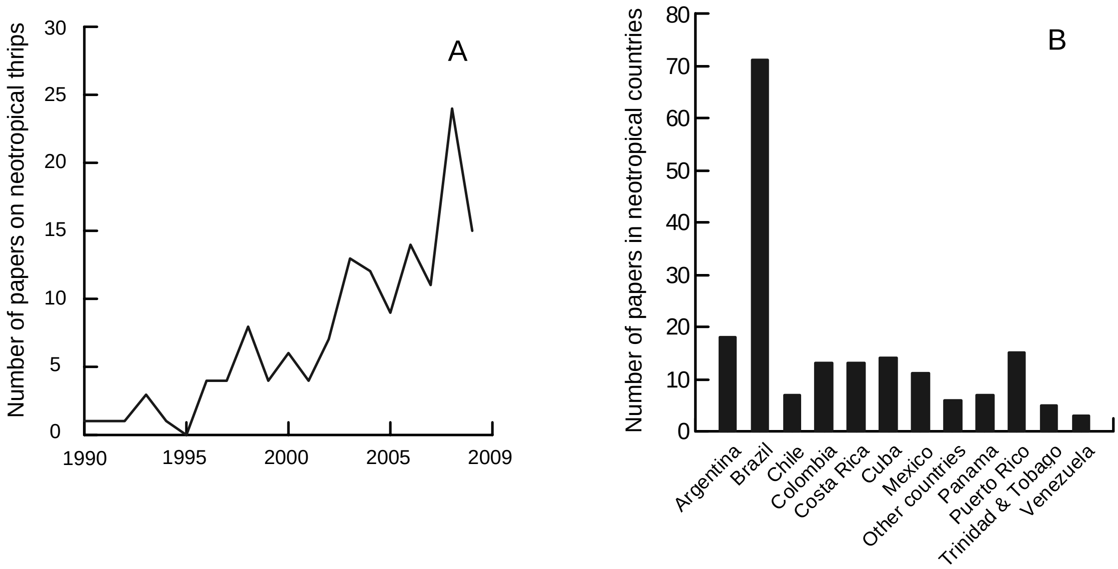

Figure 1. A) Number of papers related to Neotropical thrips over the last 20 years. B) Countries more productive in thrips studies. Other countries refer to Bahamas, Bermuda, Guadeloupe, Martinique, Paraguay and Peru with one paper each and Honduras, Jamaica and Caribbe with two papers each (Source: Scielo, JStor and Web of Science internet databases).

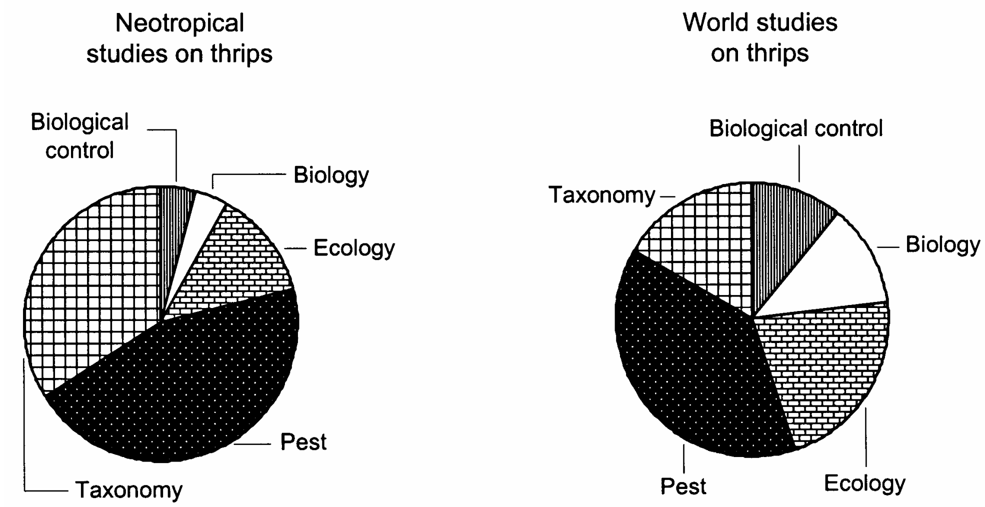

Figure 2. Comparison between published papers conducted in Neotropics and other parts of world (mainly temperate zones) related to thrips. The second chart displays New Zealand, Germany, Netherlands, Canada, England, India, Australia, Japan and United States (Source: Scielo, JStor and Web of Sciece internet databases).

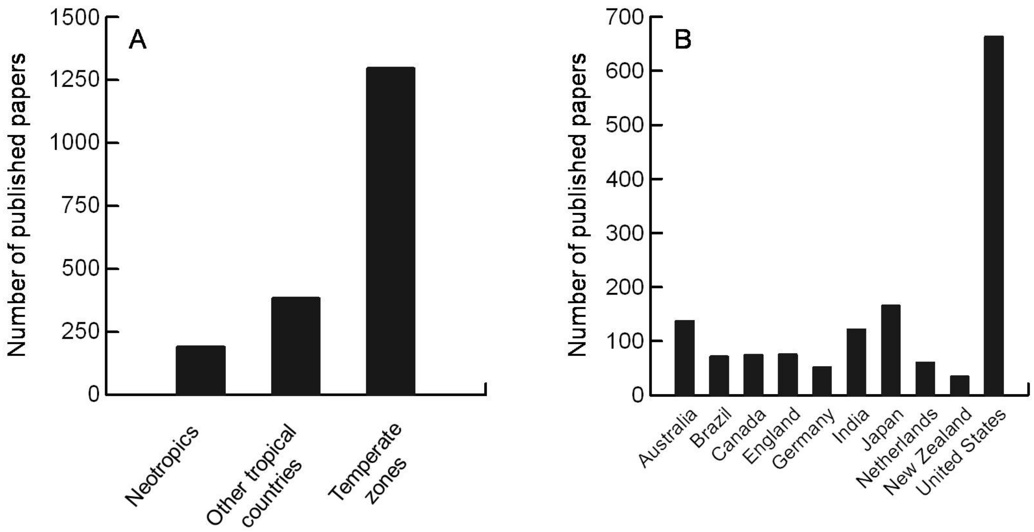

Figure 3. A) Number of published papers in the different geographical climatic zones of the world. B) Number of papers about thrips published in each country (Source: Scielo, JStor and Web of Sciece internet databases).

the great diversity present in the country but also an expression of a great amount of investment in basic and applied entomological research. Other than the United States, abundant studies on thrips were performed in few countries, of which Brazil is the most representative from the Neotropics (Figure 3B).

In this review we present a general overview of thrips ecology and biology and make available information on the current knowledge on thrips habits and habitats in the Neotropics. Additionally, we gather information on other tropical areas, such as Australia and South Asia whenever necessary in order to enrich a given topic or assumption. We compiled as much information as possible, from local to wide published papers and aim to shed light and provide an insightful assessment on the ecology and behavior of these long ignored insects in one of the most biologically diverse ecozone in the planet, the Neotropics.

Thrips - An introductory general view

Thrips are small, opportunistic, vagile, and ubiquitous insects with an adult body size ranging from about 0.5 mm to 15 mm in length and generally yellow, brown, or black in color [18, 19]. Almost 6000 species of Thysanoptera are recognized worldwide comprising 770 genera in nine families: Phlaeothripidae, Thripidae, Merothripidae, Adiheterothripidae, Fauriellidae, Uzelothripidae, Melanthripidae, Aeolothripidae and Heterothripidae [20, 21]; the occurrence includes the tropical, subtropical and temperate regions [22]. Thysanoptera feed on a variety of substrates, up to 50% being mycophagous either on spores or on hyphae and a large number feeding primarily in flowers [18]. Few species feed only on leaves [17], mosses and ferns, and there are a few predatory species [23, 24]. Polyphagy may also be found in some species [25]. In addition to these widely disparate feeding habits, thrips exhibit a diverse array of life styles including various levels of sociality [26, 27], remarkable structural polymorphisms within and between sexes [28], gall-induction on leaves [29], pollination associations [30], ectoparasitism [31, Alves-Silva & Del-Claro unpub. data] and virus transmission on crop plants [32]. Intertwined with this astonishingly broad range of niche occupation there is an inherent opportunism that allows many species to readily adopt and utilize a variety of resources in ephemeral and/or stable habitats [19, 33].

Thrips diversity in the tropics

Thrips are more diverse in the tropics and neotropics than in temperate regions. The total number of described species from Central and South America is about 2000. Studies show that Mexico has 300 species, the same number as Costa Rica and Panama [18]. Recent reports show that Argentina has approximately 120 species [34], and that Brazil has 700 species [1], the same number as Australia [35], despite the fact that there are many more entomologists and thrips researchers in Australia than Brazil.

Studies from Brazil are largely centered on taxonomic and agricultural aspects of thrips biology [36]. Studies on ecology are rare but include good examples. In Brazilian savanna the newly discovered thrips *Heterothrips peixotoa* Del-Claro, Marullo & Mound, 1997 live inside the flower chambers of *Peixotoa tomentosa* A. Juss. (Malpighiaceae) where they are safe from predatory ants [12]. In Galery Forest, *Frankliniella longispinosa* Moulton, 1933 co-occur with Staphylinidae beetles in *Faramea cyanea* Müll. Arg. and used this host plant for food and as a reproductive site [37]. In Brazilian savanna thrips are present in virtually all flowering plants. In an inventory in this region, 30 plant species (13 families) were found to support thrips from four families (Table 1). The analysis took into account the presence and absence of extrafloral nectaries on the plants as well as the color of the flowers. Most thrips belonged to the order Terebrantia. There was a relationship between the flower size and the abundance of thrips, and most species occurred in plants with yellow flowers and those without extrafloral nectaries, possibly because ants protect these plants against herbivores [38].

Published records of thrips hosts in natural areas were available from only a few locations. In Southern Brazil 61 species of thrips from four families were found in a sampling of 72 plant species (26 genera) [15]. Subsequent studies showed that thrips occupy wide disparate niches such as branches, flowers, grass tussocks and leaf litter though most diversity and abundance was verified from flowers while leaf litter presented more exclusive species [39]. Similar number of species was found in Colombian savanna where 79 thrips species (23 genera) were found in a sampling covering 30 municipalities, comprising plant families such as Asteraceae, Melastomataceae, Ericaceae, Clusiaceae, Fabaceae, Bromeliaceae, Solanaceae and Rubiaceae [40].

In some cases, economic motivations have lead researchers to seek understanding of the natural hosts of thrips considered pests in order to better understand the places thrips survive in the intercrop periods. In Argentina a sampling covering 58 species of spontaneous growing plants showed that the pest thrips *Franklineilla occidentalis* Pergande, 1895 used 57 of these plant species as a secondary host, allowing it to survive and persist throughout the year and reinfest crops when

Table 1. Thrips host plant species in the Brazilian Savanna (Color – color of petals; EFN – extra floral nectaries, if present or not; Thrips families: Thrip – Thripidae; Hetero – Heterothripidae; Phlaeo – Phlaeothripidae; Mero – Merothripidae).

Host family	Host species	Color	EFN	Thrips family
Asteraceae	*Eupatorium laevigatum*	White	No	Hetero, Thrip
Bignoniaceae	*Jacaranda rufa*	Red	No	Thrip
	Memora pedunculata	Yellow	No	Thrip
Caryocaraceae	*Caryocar brasiliensis*	Yellow	Yes	Thrip
Fabaceae	*Senna velutina*	Yellow	Yes	Thrip, Hetero
	Camptosema coriaceum	Red	Yes	Thrip, Mero
Ochnaceae	*Ourateia spectabilis*	Yellow	Yes	Thrip, Hetero
	Ourateia hexasperma	Yellow	Yes	Thrip
Rubiaceae	*Palicourea rigida*	Yellow	No	Thrip
	Declieuxi fruticosa	White	No	Thrip, Hetero
Rutaceae	*Hortia brasiliana*	Red	No	Thrip
Scrophulariaceae	*Buchnera lavandulaceae*	Red	No	Phlaeo, Thip
	Esterhyza esplendida	Red	No	Thrip
Styracaceae	*Styrax ferrugineos*	Yellow	No	Unidentified
Vochysiaceae	*Vochysia cinnamomea*	Yellow	No	Thrip
	Qualea multiflora	White	Yes	Thrip
Erythroxylaceae	*Erythroxylum deciduum*	White	No	Thrip
Myrtaceae	*Eugenia involucrata*	White	No	Thrip, Hetero, Phlaeo
	Myrcia rubella	White	No	Thrip, Hetero
Melastomataceae	*Miconia albicans*	White	No	Thrip
	Miconia fallax	White	No	Thrip
Malpighiaceae	*Byrsonima intermedia*	Yellow	No	Unidentified
	Byrsonima coccolobifolia	Yellow	No	Unidentified
	Peixotoa tomentosa	Yellow	Yes	Hetero
	Banisteriopsis stellaris	Yellow	Yes	Unidentified
	Banisteriopsis malifolia	Red	Yes	Phlaeo, Thrip
	Peixotoa cardistipulla	Yellow	Yes	Phlaeo,Thrip, Hetero
	Heteropteris ecallonifolia	Yellow	Yes	Thrip, Hetero
Bombacaceae	*Eriotheca gracilipes*	Yellow	Yes	Thrip

conditions permit [11]. In Venezuela the presence of the bean pest, *Thrips palmi* Karny, 1925, was recorded on various wild plants in order to verify secondary hosts used during the year. These results were used to develop a more effective pest management strategy [41]. This type of study is economically important because, informed pest management strategies may, for example, select host plants which support predatory thrips, like *Aeolothrips* which can spread to surrounding crops and act in biological control [33].

Patterns of occurrence in different hosts

Most biologists think of thrips as living primarily in flowers and indeed these are the thrips most easy to find but at least half of the members of Thysanoptera are not associated with flowers at all [18]. Besides feeding on flowers tissues and reproductive structures [12] thrips also occur on leaves [17, 42] and fruits [43]. In general thrips on these structures are herbivorous species which inflict damage on cultivated plants and increase their populations in relation to the availability of food types. In turn, population booms of herbivorous thrips attract predatory thrips which benefit from the gregariousness behavior of prey and stay within the colonies where prey is abundant, as happens in *Persea americana* Mill. cv. Hass (Lauraceae) in Mexico [44]. In this case, interestingly the entire plant, such as flowers, leaves and fruits hosted thrips, which is uncommon. Many thrips species, besides being polyphagous, are specialized on particular host structures, for example the flower-living genus *Heterothrips* [18]; and only a few species can in fact feed on flowers and leaves concurrently, or also include the fruits in its diet, like the polyphagous *F. occidentalis*, which is also omnivorous [45].

Thrips can exhibit different patterns of occurrence depending on the variety of the host species. In *Prunus persica* (L.) Batsch. (Rosaceae) there is a predominance of *Frankliniella* species whereas in *Prunus persica* var. *nuscipersica* (Suckow) C. K. Schneid. the genus *Thrips* is the principal one [46]. However in the absence of *Thrips*, the species of *Frankliniella* are predominant in both *P. pesica* and *P. persica var. nuscipersica* and indeed they cause more severe injuries than *Thrips* [10, 43]. All these studies were carried out in Brazil and the compiled information for the thysanopterofauna present in *P. persica* included 16 species of thrips which occurred on fruits, flowers and leaves.

Utilizing different food sources, such as leaves, fruits and flowers demands a high flexibility of feeding apparatus and digestion of plant tissues [19] and the species which possess these features are highly invasive and capable of rapid accommodation in a new host. Because thrips dwell in many microhabitats they are consequently subject to host plant phenological changes. These changes are driven by the environment, since weather imposes conditions that determine when a plant will produce flowers, fruits and leaves [22].

In *Persea americana* Mill. a severe winter with temperatures near 10ºC corresponded with low levels of thrips abundance in January, whereas the high temperatures in June (25.8ºC) evidenced a boost in thrips numbers. However the authors did not find any relationship between the climate and thrips [44]. Instead these insects were more abundant during the summer because this is when their host plant flowered. Similar results were found for *Haplothrips heliotropica* Mound & Zapater, 2003 living on *Heliotropium amplexicaule* Vahl (Boraginaceae) however, in this case thrips underwent winter diapauses [14]. In cassava, *Scirtothrips manihoti* Bondar, 1924 populations decreased in the dry and cold season probably due to leaf senescence of host [47]. Weather did not influence thrips abundance and similar results were later found for thrips on cabbage [48].

In all these studies the influence of environment on thrips populations seems to be indirect because weather influences thrips host plant phenology such as production of flowers and leaves which in turn attracts and maintain thrips in a given host. Thrips infestation increases as plants produce more flowers, shoots and young leaflets; on the other hand, as the production on these structures decreases, the infestation by thrips also declines. This situation has been clearly demonstrated in pollinating thrips species. During times when flowers are abundant, thrips occur in large numbers but when flowering ceases, thrips populations survive only in low numbers in scattered host plants [49, 50].

Thrips pollination in tropical plants

Thrips can be effective or accidental pollinators, mainly due their habits of commonly feeding on pollen, nectar and floral tissues [51]. In the course of evolution, shifts from simple ‘‘floral predators’’ to pollinators might have occurred several times [30]. Odors seem to be an important floral attractant for thrips, particularly in Neotropical Annonaceae. The thrips pollinated species of Annonaceae have whitish and erect flowers, their floral odor is pleasant and sweet and thrips may act as exclusive or effective additional pollinators. Accidental pollination occurs, for example, in *Bocageopsis multiflora* (Mart.) RE. Fries, *Xylopia aromatica* (Lam.) Mart., *X. amazonica* RE. Fries and *Oxandra euneura* Diels, all of which are present in the Neotropics, with great abundance in Amazonian forest and Brazilian savanna [52, 53, 54]. Annonaceae species with white or yellowish-white, small, delicate, day-active flowers, may be pollinated either solely by thrips, or by a combination of thrips and small beetles [55]. This interaction with Annonaceae gets more interesting if we take into account the protogynous characteristic of many flowers in which the pistillate and staminate phases occur on different days suggesting that thrips must visit and migrate from flowers in different days in order for pollination to occur [54].

Thrips also promote pollination in the androdioecius plant *Castilla elastica* Sessé ex Cerv. (Moraceae) in a seasonally dry forest in Panama. In this plant staminate and pistillate flowers occur on different inflorescences of a cosexual plant. In addition, inflorescence structure of staminate inflorescences on males, and staminate and pistillate inflorescences on cosexes are noticeably different and this dissimilarity may reflect special roles and requirements of the inflorescences in pollination. The most abundant flower visitors were *Frankliniella diversa* Hood, 1935 and *F. insularis* Franklin, 1908, which accounted for 99.0% of flower visitors and all of which carried pollen grains effectively [30].

The number of plants pollinated by thrips is likely underestimated in the Neotropics. Nevertheless, most published papers do not present data of thrips behavior in regards to pollination and therefore provide only occurrence registers of thrips for a given plant [34, 56, 57] or list these insects as associated with reproductive structures [25, 34, 58]. This situation is more common in crop plant species, where the main concern is to manage pest populations rather than verify thrips behavior, or a potential role in plant pollination. This issue is particularly important, because thrips proved to be an effective pollen vector for many flowering plants and are believed to have had a significant role in the evolution of the angiosperm flower [59]. As more attention is given to thrips activities and behaviors, more discoveries are being made which reveal their potential as pollinators [60].

Pest status in the Neotropics and transmission of tospoviruses

Thrips are among the furtiveness insect invaders either due to their small size or because of their cryptic habits and flight dispersal. Major economic damage results from establishment, proliferation and spread of thrips and their associated plant virus [19, 61]. Though very scarce, in the literature on neotropical thrips it is possible to find at least one paper from each country in which authors report certain species of thrips as crop pests, and in certain cases, these are the unique records of thrips in that country.

The species of *Frankliniella* and *Thrips* are the main crop pests in the neotropics. Most papers treat these species in several approaches, from taxonomy, simple occurrence to attack on plants and biological control [56, 62, 63, 64]. In Colombia *T. palmi* aggregations cause considerable damage in dry beans (*Phaseolus vulgaris* L. cv. Morgan (Fabaceae)) [65] whereas in Equador and Bolivia the genus *Frankliniella* is responsible for the highest damage in potatoes and ornamental crops [66]. The Tomato Spotted Wilt Virus (TSWV) is a very damaging disease to tomato crops in Paraguay [67] and in Uruguay tomatoes become stunted and have yellowed leaves. Necrosis and characteristic ring spots are observed on stems and fruits respectively [68]. In Puerto Rico, thrips attack leaves and flowers of soybean *Glycine max* (L.) Merrill (Fabaceae), causing injury through feeding and transmission of tospoviruses [69].

In Argentina, tospovirus diseases are known as “Peste Negra” [70] and may cause yield losses up to 80%. The wide dispersion of tospoviruses type GRSV (Groundnut Ringspot Virus) may be related to the spread of *Frankliniella schultzei* Trybom, 1910, which transmits this virus more efficiently than other vectors [71].

In Brazil, the records of pest thrips are more disseminated and about 24 species are considered to damage cultivated plants [36]. Similarly to the other countries, the most representative genera are *Frankliniella* and *Thrips*, which feed on a variety of different plants such as onion, garlic, tomato, etc. [72].

Compared to northern countries, the spread and presence of tospovirus in the tropics seems to be more aggressive. This may be a result of the behavior of the main vector, *F. occidentalis*, also known as the western flower thrips. This species does not overwinter in the tropics due the high temperatures in the region and can reproduce quite well throughout the year [33]. As only larvae are capable of hosting the virus and inoculating plants [73], the continuous breeding of *F. occidentalis* in the tropics remains as a serious problem in many crops and greenhouses, causing huge economic losses [62].

The damage caused by pest thrips in the tropics needs to be assessed very carefully and precautions need to be assigned in order to suppress the population peaks of these insects [74]. Tropical countries are important producers of fruits and vegetables and the economies of these countries are partially dependent on exportation of these crops [75, 76]. Thrips attack causes huge economic losses every year. The control and management of pests is difficult because chemicals and biological agents to suppress thrips populations demands substantial financial input. Additionally, due their rapid reproductive cycle, with several generations in the same year or season, thrips have been continuously developing resistance to pesticides and biological control agents which often fail to control thrips populations on crops [77, 78].

Thrips feeding versus plant defenses and nutritional value

Even within the papers dealing specifically with pest thrips we find high levels of diversity in the way thrips attack the host plants, given that these insects can feed on leaves, petals, reproductive structures and fruits in many different habitats [18]. Such feeding flexibility and habitat infidelity is possible because thrips species are generally not constrained by highly specialized evolutionary relationships with particular species of host plants, fungi, or prey [19] and it is also interesting the way some thrips are not affected by plant defenses.

High levels of herbivory were noticed in *Didymopanax vinosum* (Cham. & Schltdl.) Seem. (Apiaceae) and the main herbivore was *Liothrips didymopanacis* Del-Claro & Mound, 1996 [17]. This thrips was found throughout the year and leaf injury occurred when leaves were still young. By scraping and sucking from the leaf surface, this insect caused necrosis and twisting of the leaf. Apparently this thrips species was not affected by nutritional and defensive compounds of the plant. In cassava (*Manihot esculenta* Crantz var. Cacau) the thrips species *S. manihoti* was not affected by leaf compounds like nitrogen and potassium and no direct effects of climatic factors were observed influencing thrips population [47]. The same situation was observed for *T. palmi* in relation to leaf compounds of the eggplant *Solanum melongena* L. (Solanaceae) [48].

Generally plants subject to stressful weather conditions may support more thrips than those raised in controlled climates. For instance, eggplant plantations in regions with higher temperature variation have problems with *T. palmi* [48]. Eggplant has been selectively bred to standardize and increase in productivity. This process has resulted in the loss of compounds and glandular tricomes which played an important role on the resistance to herbivores. Plants adapted to certain conditions have so little nitrogen available in their tissues that they are an inadequate source of food for young herbivores attempting to feed on them. Any departure from the normal conditions such as high temperature variation or water stress, upsets the metabolism of the plant and may increase the availability of nitrogen in its tissues, thus potentially powering increased survival and abundance of herbivores feeding on those tissues [79, 80].

Successful interactions of thrips with their host depend on a complex set of environmental and behavioral factors that considerably influence the fitness and physiology of insects. Modifications of any of these factors equally influence the suitability of any plant as a host [25]. As food specialization tends to result in host specificity, thrips, as do other insects, respond in diverse ways to changes such as aging, water stress, concentration of nutrients, etc., that occur within the plants [22].

Gall induction and sociality

An estimated 13000 species of insects induce galls, structures composed of plant tissue within which the insect feeds and shelters [81] and galling thrips are represented by about 300 species belonging to 57 genera, almost all of them belonging to the tubuliferan subfamily Phlaeothripinae [82]. Gall induction results from the concentrated feeding of one or more individuals at one or more sites on the leaf, typically a male and a gravid female feeding at the early bud stage, when tissues are not sufficiently differentiated [83].

Little is known about galling thrips from neotropics and tropics, most of which are recorded from Australia [28] where gall-formers are found in the arid and semiarid interior [27]. Cecidogenous thrips predominantly occupy tropical and subtropical regions and almost 85% of the known species of gall thrips occur in peninsular India, Indo-Malaysia, Indonesia and Northeastern Australia [22]. In Central and South America, the genera *Holopothrips* and *Liothrips* are known to include various gall-inducing species [18].

In Brazil *Holopothrips claritibialis* Cavalleri & Kaminski, 2007 was found feeding on leaves of *Mollinedia schottiana* (Sprengel) Perkins (Boraginaceae) but did not form galls [84], however closely related species *H. conducans* Priesner, 1921, as well as *Gynaikothrips*, *Haplothrips*, *Leptothrips*, *Liothrips*, *Pseudophilothrips* and *Trybomia*, were found to inflict galls, although their hosts are not well known [36]. The first register of gall-making thrips in Neotropics dates from the 1960s. The species *Mixothrips priesneri* Costa Lima was collected in leaf rolls of *Eugenia* sp. (Myrtaceae) but no information about its life history was described [85].

Gall-forming thrips exhibit a suite of traits suggestive of the presence of complex social behavior, such as male forelegs related to fighting, female dimorphism suggesting behavioral differences, and physogastry which denotes large females capable of high fecundity and laying-egg capacity [27]. Moreover thrips comprise the only order besides Hymenoptera where females are diploid and males are haploid. This makes them useful subjects for studying the roles of kin selection and ecology in social evolution [26, 86].

Unfortunately social behavior in thrips in the Neotropics has not been well studied with only a single report from Panama. The species *Anactinothrips gustaviae* Mound & Palmer 1983, is an advanced parasocial thrips found in colonies which reproduces communally [87]. Food supply was the primary factor which has promoted the evolution of advanced social behaviors in this species contrary to most other thrips species.

The knowledge of gall inducing and social thrips in the Neotropics may be an additional tool in providing clarification of the evolution and spread of this behavior as well as the adaptations that enable thrips to occupy a wide range of plants, resist different predators and survive in a variety of environmental conditions.

Thrips interactions with other arthropods

Although being known for its herbivory in many plants, thrips also feed on animal tissues, particularly other thrips or mites [18]. For instance, the omnivorous species *F. occidentalis* may feed on spider mites or plant tissues depending on availability in their habitat [45]. Some genera are obligate predators of other thrips, spider mites and lepidopteran eggs, like the pantropical *Franklinothrips* [23]. Species in this genus mimic ants with both behavior and body form, many having been observed to run very actively and to palpate the substrate with their antennae [24].

The most remarkable example of thrips predation is exhibited by the behavior of the ectoparasitic species *Aulacothrips dictyotus* Hood, 1952.These thrips parasitize hemipteran species such as *Aetalion reticulatum* L. 1797 (Aetalionidae) and *Enchenopa brasiliensis* Strümpel (Membracidae) in Brazil [31, Alves-Silva & Del-Claro unpubl. data]. Thrips larvae seem to be obligate parasites while adults are free-living. The hemipterans may serve also for dispersal transporting to other hemipteran aggregations and plants [Alves-Silva & Del-Claro unpubl. data]. Thysanoptera are a group with noteworthy habits and there is no intrinsic reason to consider the ectoparasitic way of life as impossible for thrips, from either the nutritional or the behavioral perspective [88].

The large biomass of thrips in the tropics is evidence that these insects are an important food resource for other animals, however, because of their small size, their natural predators and parasitoids are known only imperfectly [18]. The genus *Orius* (Hemiptera: Anthocoridae) comprises species that are mostly predators on thrips in natural and managed ecosystems [16]. In South Africa *Heliothrips haemorrhoidales* Bouché, 1933, and *Selenothrips rubrocinctus* Giard, 1901 are two of the main pests on avocado and are biologically controlled by the predator *Orius tripoborus* Hesse and the parasitoid wasp *Tripobius semiluteus* Boucek (Hymenoptera: Eulopidae). The adult wasp female inserts her eggs singly in the body cavity thrips larvae and grows rapidly filling the entire body cavity of its host [89]. In an inventory in Argentina thrips natural enemies were found in 22 from 58 plants sampled. The most frequently observed predators were the phytoseiids *Neoseiulus californicus* McGregor and *Phytoseiulus macropilis* Banks and the ascid *Asca* sp. But the most abundant predator was *Orius insidiosus* Say 1832 which was very common on species of Asteraceae [90].

The studies on the natural enemies of thrips started out of a necessity to control pest species in agroecosystems and have begun to supplant the use of chemicals in crops. However, because of the patchy distribution of high-density populations and the occurrence of life stages that occupy widely varied niches, thrips are an unstable resource for their natural enemies [19] and predators generally inflict low levels of mortality [91].

CONCLUSIONS AND PERSPECTIVES

The tropics are the most biologically diverse region on the planet [92] and support thousands of unique thrips species. These species present amazing interactions with plants ranging from simple herbivory to complex mutualistic pollination relationships [18]. The neotropics offer abundant opportunities to study the varied interactions of thrips, their ecology and diversity. There are many papers concerning purely descriptive records of new species [93, 94], but the number of studies that combine species description with natural history approaches is rising [14, 84]. If we are to develop an understanding of the biology and origin of thrips diversity the neotropics, we need to explore the combination between taxonomy and ecology [1]. More important is being the great effort from financial agencies in natural sciences in the last years by providing funds for undergraduate and post graduate students interested in studying biodiversity and conservation, particularly in Brazil. Multidisciplinary studies may also contribute to the understanding of the many aspects regarding population dynamics and responses to environment, as well as alternation of hosts and the intrinsic and extrinsic factors accountable for thrips persistence in crops and natural areas. Comprehensive biodiversity studies clearly require many years of well funded observation by a range of biologists [95]. Progressively evidence is being provided that thrips are not just ubiquitous irritants to be sprayed with pesticides, but are interesting organisms with varied and complex biologies [1, 28].

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