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Taxonomic and Functional Structure of Phytophagous Insect Communities Associated with Grain Amaranth

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Abstract

Amaranthus are worldwide attacked mainly by leaf chewers and sucker insects. Stem borers and leaf miners follow in importance, while minor herbivores are leaf rollers, folders, and rasping-sucking insects. The herbivorous community observed on *Amaranthus* spp. in Argentina was consistent with the information reported worldwide both in guild composition and order proportion. Amaranth plants had a higher number of phytophagous species in their native rather than in its introduced range. Occurrence of insect guilds differed in space and time. The highest density of leaf chewers was observed shortly after the emergence of plants, while higher density of borer and sucker insects coincided with reproductive stages of the crop. The sucking guild was observed mainly at panicles, while the insects within the leaf chewer group were registered in both leaves (92.6%, n=746 adults) and inflorescences (7.4%). The borer guild was also recorded in stems and inflorescences; however, the density of larvae in stems was about four times as high as the density observed in panicles (n=137 larvae).

Introduction

In the last decades, amaranth has received renewed interested as a food crop. This is largely due to the high amounts of good quality proteins for human consumption contained in its grains (Downton 1973, Teutonico & Knorr 1985). Its amino acid profile, and in particular the high levels of lysine, makes amaranth grains an attractive protein source, very similar to the recommended amino acid pattern required for human nutrition, as established by FAO and the World Health Organization (Becker *et al* 1981, Pedersen *et al* 1990). Moreover, being a pseudocereal, grains of amaranths lack gluten, thus being a suitable food for people with gluten intolerance (Zannini *et al* 2012). But *Amaranthus* plants are not only recognized for their nutritional features but also due to their ability to thrive in many environments and tolerate adversities such as low water regime (Liu & Stützel 2002), poor soils, and moderate salinity levels (Omami & Hammes 2006), conditions on which other commercial crops are not able to grow (Brenner *et al* 2000, Johnson & Henderson 2002).

Numerous herbivorous insects have been reported to affect the *Amaranthus* genus worldwide (El-Aydam & Bürki 1997). Among them, species of leaf chewers and sucking insects are known to feed heavily on leaves and floral buds (Bürki *et al* 1997, Olson & Wilson 1990), whereas the stem borer guild is mentioned as the prevalent group at global scale (Louw *et al* 1995). Leaf miners, leaf rollers, and leaf folders are also mentioned as amaranth insect feeders. For the first group, species are usually reported in *Amaranthus* wild plants rather than in crops (Stegmaier 1950, Spencer 1973, Mujica & Berti 1997, Carrasco 1987), while little is known about the species in the leaf roller and folder guilds (Jena *et al* 2000, Waterhouse 1994). Although *Amaranthus* is a genus that is widely distributed around the world, most of the species (including those cultivated for grain purpose) have originated in the Americas (Sauer 1950, 1967, Coons 1982), while only a few of them are native to Europe, Asia, and Africa (Sauer 1967, Robertson 1981, Costea *et al* 2001).

For it being an introduced crop in many non-American countries, grain amaranth might experience a reduction of herbivorous insect richness in introduced ranges according to the "enemy release hypothesis" (ERH) (Keane & Crawley 2002). This would represent an advantage for its cultivation in non-natural areas. However, comparative studies regarding herbivore diversity, load, and herbivory damage on *Amaranthus* spp. in the Americas and elsewhere are not available. In turn, few studies concerning phytophagous insects on grain amaranth has been published in South America (Ves Losada & Covas 1987, Guerrero *et al* 2000, de Oliveira *et al* 2012, Riquelme *et al* 2013), which is considered the original region of two cultivable species *Amaranthus cruentus* and *Amaranthus mantegazzianus* (Sauer 1950, 1967). Therefore, the first aim of this study was to inventory and describe the community of phytophagous insects associated to grain amaranth in Argentina, exploring the occurrence of insect guilds along the phenological cycle of the crop. The second aim was to compare the *Amaranthus* phytophagous insect fauna in American and non-American countries on the basis of a literature survey, focusing the analysis on its taxonomic and guild structure.

Material and Methods

Field surveys

Field surveys of phytophagous insects were conducted in crops of three amaranth species (*Amaranthus cruentus* cv. Don León, *Amaranthus hypochondriacus* cv. Artasa 9122, *A. hypochondriacus* San Antonio, *A. hypochondriacus* FK 280-FH1, and *A. mantegazzianus* cv. Don Juan) sowed in the north of Santa Rosa, La Pampa, Argentina (36°37′S, 64°16′W), during two growing seasons (summer 2007–2008 and 2008–2009). A field of 156 m^2 was sowed with a space of 0.50 m between rows and a density of 3.5 kg of seeds per hectare. The plants did not receive any insecticide application and weeding was done manually. The essay was located in a livestock area characterized by grasslands, wheat, and alfalfa field crops. During two growing seasons, the essay was performed in a field of 7 ha in which several weeds were present, being *Cynodon dactylon*, *Digitaria sanguinalis*, *Portulaca oleracea*, *Xanthium cavanillesii*, *Salsola kali*, and *Conyza bonariensis* the most abundant.

Insect sampling was conducted shortly after the plant emergence and through all the crop cycle. Five samples in the first year and seven in the second year were performed during daytime (9:00 AM to 2:00 PM approximately), when most of the herbivorous insects are active. On three occasions in summer 2008, observations were made at night (9:00 PM to 10 PM) to sample phytophagous insect not observed during daytime. In each sampling date, 250 plants were selected randomly and the whole plants were inspected. The insects observed were counted and collected (at least one sample of each species) for later identification in the laboratory. The growing stage of the insects and the location where they were found in the plant were also registered.

During the second year of the trial (summer 2008/2009), borer insect occurrence was recorded. For that, a total of 500 plants were taken at random in two different stages of the plant coincident with stages R4 and R6, according a phenological scale (Mujica & Quillahuamán 1989). The stalks and panicles of these plants were sectioned longitudinally, and active larvae were counted and preserved in 70% ethanol for identification.

Literature survey

A literature survey of phytophagous insects associated to *Amaranthus* spp. was carried out, including research articles, reviews, and catalogs mentioning insects on both wild and cultivated amaranth plants. Only herbivorous insects that were reported as effectively feeding on plants were considered, and they were grouped into different guilds mainly following Stork (1987).

Statistical analysis

The chi-square test was performed to compare guild structure and abundance between phytophagous communities observed in the Americas and those recorded in other parts of the world. The same analysis was performed to compare herbivore communities in Argentina with the information recorded worldwide. In all cases, an alpha of 0.05 was used.

Results

Seventy previous studies on herbivorous fauna associated to *Amaranthus* plants made in 33 countries (42 in America and 28 elsewhere) on the five continents reported 255 species of phytophagous insects. The guild of leaf chewer was the largest and richest group worldwide (El-Aydam & Bürki 1997, Clarke-Harris *et al* 2004, Aragón-García *et al* 2011), representing half of the total insect species recorded feeding on amaranth (Fig 1a). The remaining species were distributed among sucking insects (28%), stem borer (9%), leaf miner (8%), and three minor guilds: rasping-sucking insects (3%), leaf folder, and leaf roller (1% each) (Fig 1a). Species in the leaf chewer guild belonged to 21 families of insects, while the leaf folder guild was just represented by two species in one family (see Table 1 in the Online Supplementary Material).

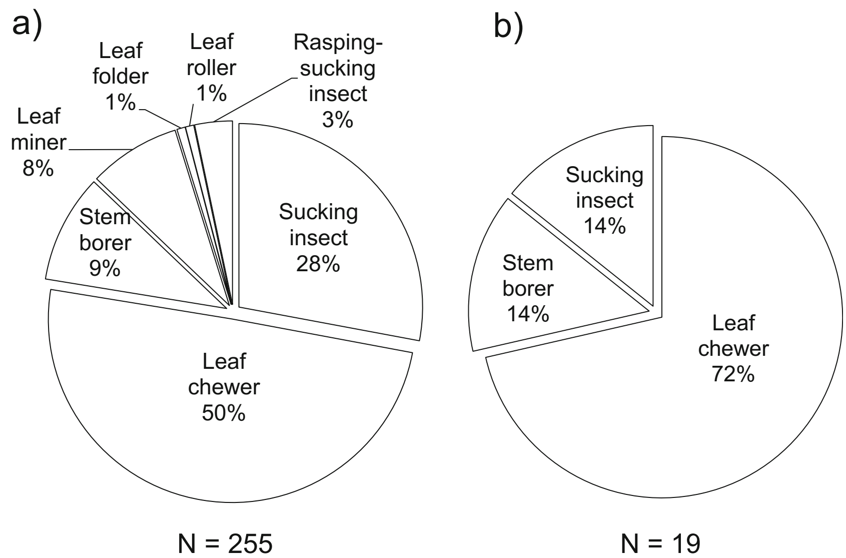

Fig 1 Guild structure of herbivorous insect assemblages associated with plants of *Amaranthus* spp. worldwide (**a**) and in Argentina (**b**).

Amaranth plants had a higher number of phytophagous species in their native than in their introduced range (χ^2_{guild}= 12.69, *df*=6, p_{guild}=0.04), the leaf chewer, the sucking, and the leaf roller guilds being represented in average by about twice as many species as in the Americas (Fig 2). In contrast, none of the species of leaf folder were present in the American continent and the number of species within the stem borer, and the rasping-sucking guilds were lower in the native range of *Amaranthus* than elsewhere. There was no difference in the taxonomic structure on herbivore communities based in the number of species in each order (χ^2_{order}= 9.59, *df*=5, p_{order}=0.08). Worldwide, the orders Coleoptera, Lepidoptera, and Hemiptera had the largest number of species cited on *Amaranthus* plants, while Diptera, Orthoptera, and Thysanoptera represented the smaller groups (Fig 3a).

In Argentina, we gathered a total of 1,759 insects feeding on amaranth plants in the two sampling periods, 44% belonged to the guild of sucking herbivores, 46% to the leaf chewer guild, and 10% were stem or panicle borers (Fig 4). The sampled insects belonged to 19 species, the leaf chewer being the most abundant and speciose guild (Figs 1b and 4a). The three species included in the borer guild behave as leaf chewer insects in adult stage.

Within the leaf chewer guild, *Epicauta adspersa* (Klug), *Achyra similalis* (Guenée), and *Naupactus verecundus* Hustache were the most abundant species representing 53%, 15%, and 13% of defoliating insects, respectively (Fig 4a). The pentatomid *Chinavia musiva* (Berg) was the most common insects among sucking herbivores representing 99% of the individuals in this group (Fig 4c), while *Conotrachelus histrio* Boheman, *Conotrachelus cervinus* Hustache, and *Aerenea quadriplagiata* Boheman were the only three borer species found (Fig 4b).

The three borer species were observed in the evening hours, and both *C. histrio* and *C. cervinus* were always observed in pairs in mating activities.

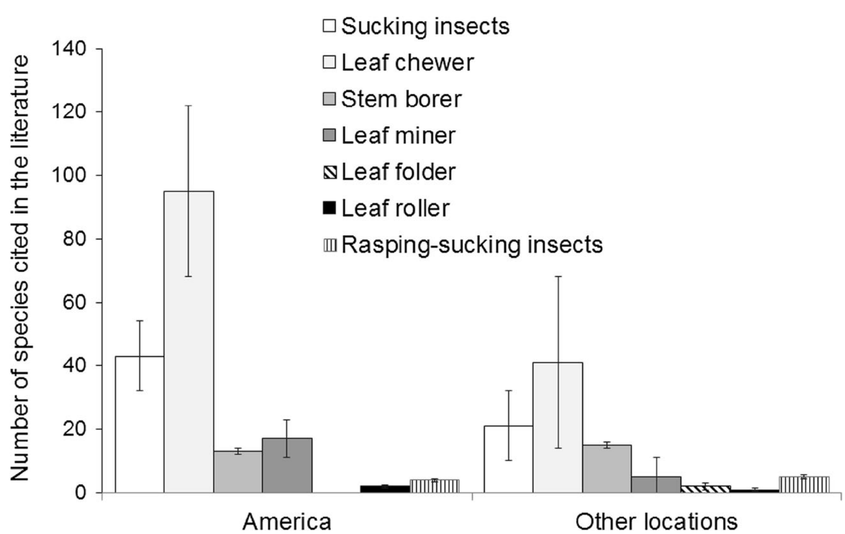

Fig 2 Comparison of insect species guilds associated to *Amaranthus* spp. in their native and introduced ranges. *Error bars* represented ± standard error.

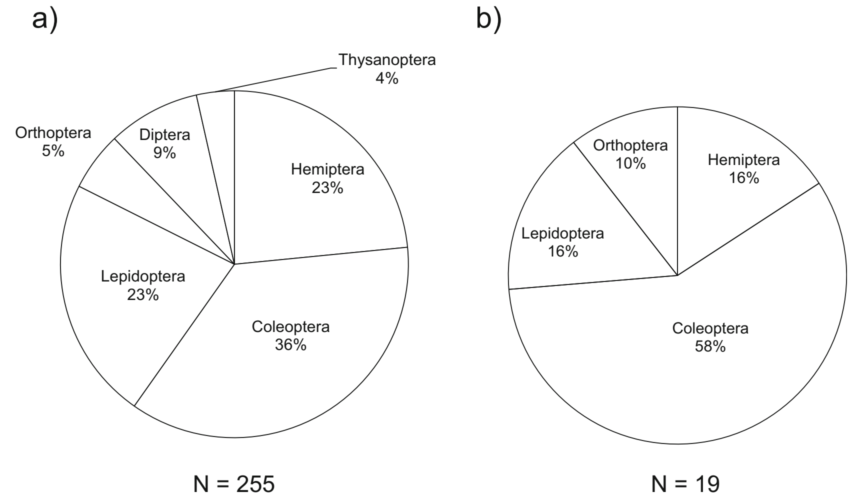

Fig 3 Taxonomic order of insect species cited in plants of *Amaranthus* spp. worldwide (**a**) and observed in amaranth grain in Argentina (**b**).

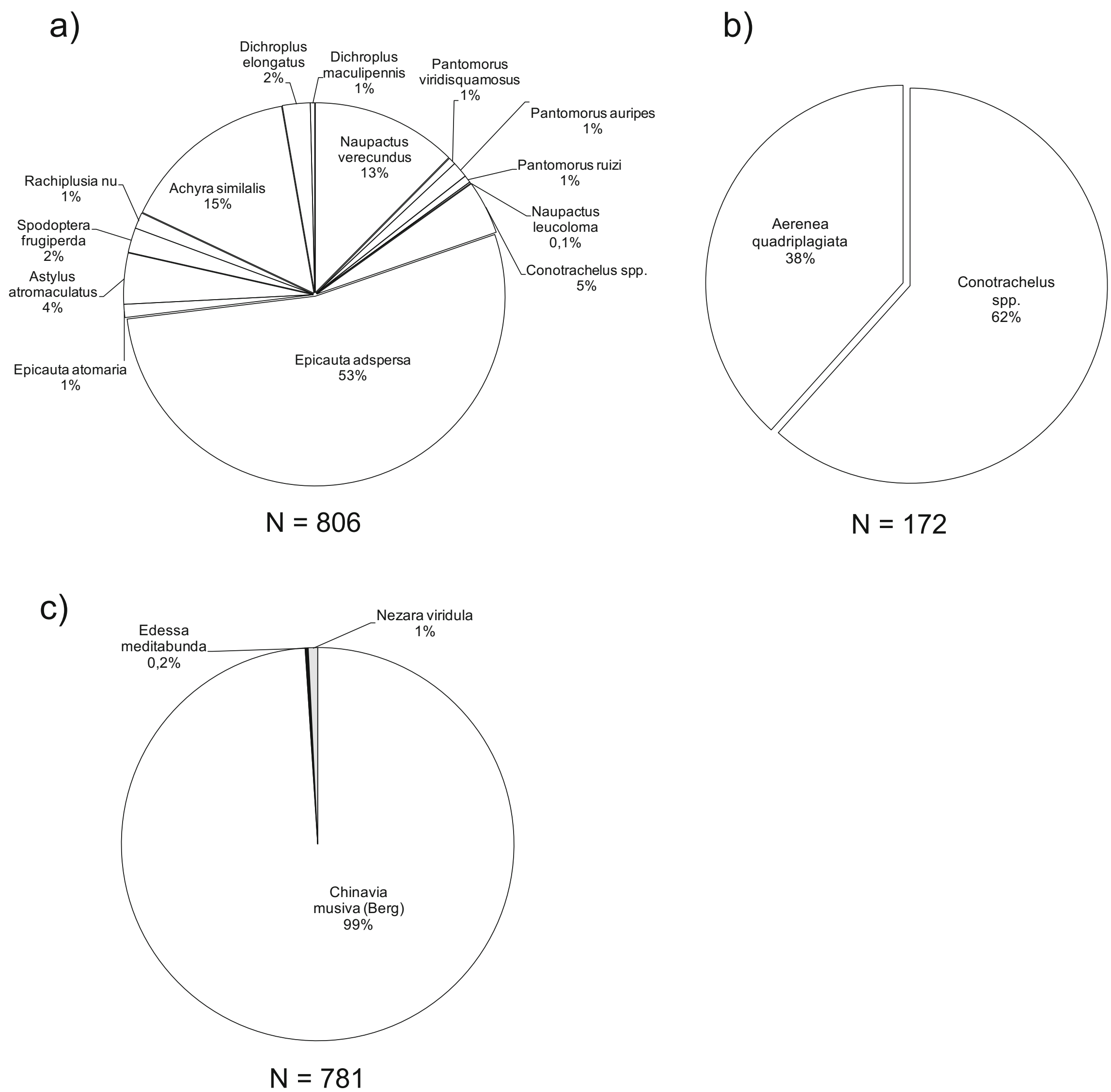

Fig 4 Insect species observed feeding in *Amaranthus* plants in Argentina: **a** leaf chewers, **b** stem borers, and **c** sucking insects.

The sucking guild was observed at panicles while those insects included as leaf eaters were registered in both leaves (92.6%, *n*=746 adults) and inflorescences (7.4%), whereas borer insects were found in stems and inflorescences. Of the total plants examined, 63.8% (*n*=319) were affected by borer insects. The density of larvae in stems was about four times as high as the density observed in panicles (*n*=137 larvae). Guild density fluctuated at different stages of crop development: the highest density of borer and sucker insects was observed in the reproductive phase of the plant, whereas leaf eater insects were recorded from emergence of the plants until physiological maturity of the panicles (Fig 5).

The herbivore community observed on *Amaranthus* spp. in Argentina did not differ from that recorded in other countries neither in guild composition (χ^2_{guild}=5.06, *df*=6, p_{guild}=0.53; Fig 1) nor in proportion of species within orders (χ^2_{order}=6.05, *df*=5, p_{order}=0.29; Fig 3).

Discussion

Community of herbivores worldwide

Leaf chewer and sucker insects are the most abundant herbivores on *Amaranthus* plants worldwide. Chrysomelidae, Noctuidae, and Curculionidae were the most important families among the chewers, while Cicadellidae and Miridae dominate the sucker guild. The stem borer and the leaf miner guilds followed in abundance, with a similar percentage of 9% and 8% of the total of insects, respectively. Both guilds were represented by few families, more than 76% of the borer species belong to Curculionidae, while a similar percentage of leaf miner species belong to Agromyzidae and Anthomyiidae (both Diptera). Even though stem borers represented a small fraction of the total insects, they usually produce severe damage on cultivated amaranth (Terry & Lee 1990, Jha *et al* 1992, Louw *et al* 1995, vdM Louw & Myburgh

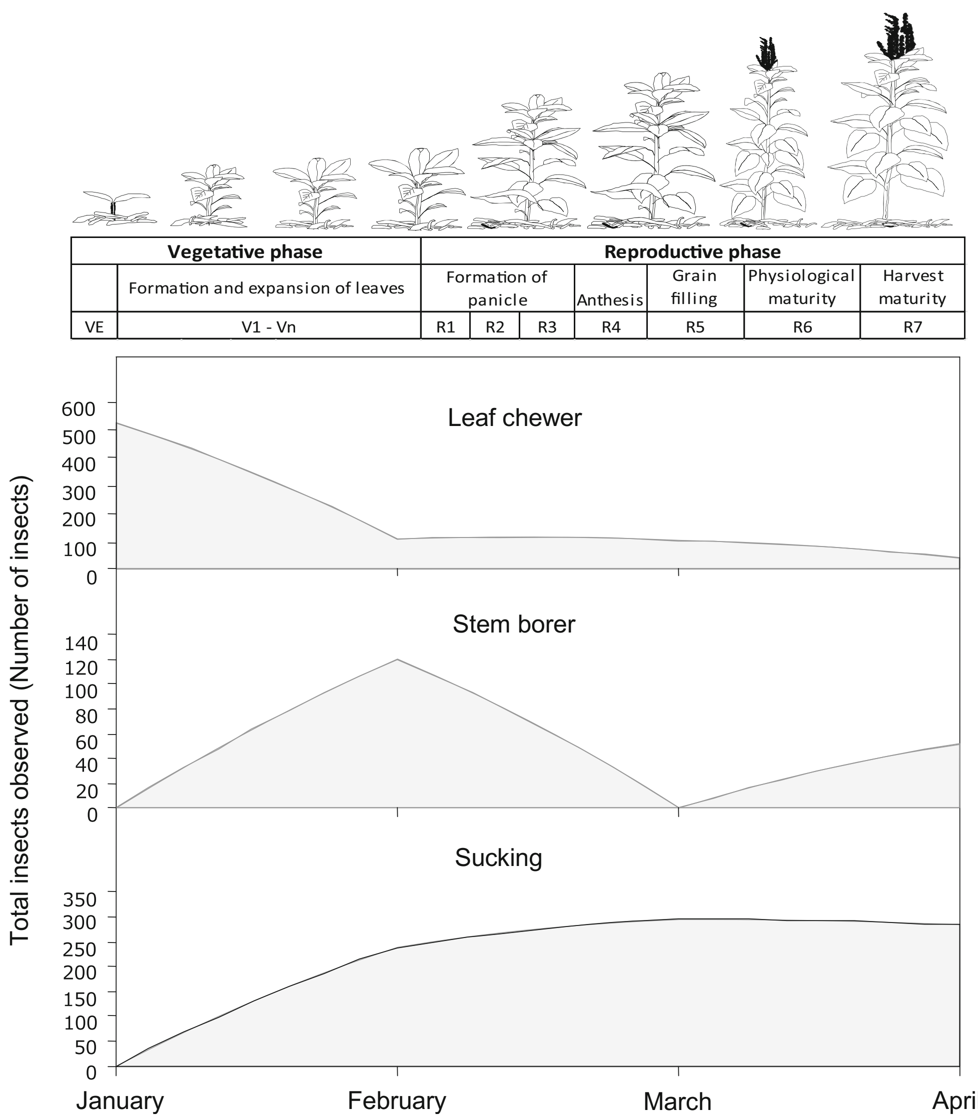

Fig 5 Occurrence and density of phytophagous guilds observed at phenological stages of plant. Appearance of plants at each stage is illustrated in *the table at the top of the figure*.

2000, Salas-Araiza & Boradonenko 2006) unlike leaf miners, which are referred mostly on wild types (Stegmaier 1950, Spencer 1969, Spencer & Havraneck 1989, Alex & Heal 1994). The stem borer guild in their larval stages makes galleries in the main stems, but depending on the species, it could also be on the smaller secondary stems, thicker leaf petioles, and even in roots (Wilson 1990, Louw *et al* 1995). In contrast, occurrence of leaf folder, roller, and rasping-sucking insects is sporadic, and scarce information related to the damages produced by these groups on *Amaranthus* crops may be found (Stegmaier 1950, Waterhouse 1994, Jena *et al* 2000).

The studies on herbivorous fauna associated to *Amaranthus* spp. indicated that amaranth plants in introduced ranges (non-American countries) seem to sustain a reduced number of herbivorous insect species within each guild (χ^2=12.69, *df*=6, *p*=0.04). Although this may be due in part to the greater number of studies conducted on the insect fauna of amaranth in America (*n*=42) than elsewhere (*n*=28), the results coincide with the predictions of the hypothesis of the release of natural enemies (Keane & Crawley 2002). The leaf miner guild showed a higher loss of species than ectophytophagous insects (chewer and sucker insects). This agreed with a previous report that indicated plants in introduced areas were less attacked by specialists and endophytophagous insects (Liu & Stilling 2006). Since they establish a close relationship with the host plant, it is expected they need more time to develop in a new host. Nevertheless, this was not observed for the stem borer guild that presented more herbivore species outside the Americas. Considering that plants of the genus *Amaranthus* are particularly vulnerable to this insect guild and several species were documented from Africa and Europe (Louw *et al* 1995, Bürki *et al* 1997, Anno-Nyako *et al* 1991, Clarke-Harris *et al* 2004, Banjo 2007, Gültekin & Korotyaev 2012), it is possible that amaranth plants may recruit new species belonging to this guild in the introduced ranges (Bürki & Nentwig 1997). Herbivore species richness in a geographic range may be influenced by many factors, e.g., geographical distribution of the plant, structure and interactions within communities, and sampling efforts, among others (Strong *et al* 1984, Colautti *et al* 2004); thus, it should be considered that the list of insects associated to *Amaranthus* is still incomplete, especially in South and Central America where minor guilds are scarcely studied, and no information about damage levels by different guilds on cultivable amaranth are available.

Community of herbivores in Argentina

Proportions of species observed for each guild and each insect order in Argentina were consistent with the reported worldwide (χ^2_{guild}=5.06, *df*=6, p_{guild}=0.53; χ^2_{order}=6.05, *df*=5, p_{order}=0.29). Only the three most important guilds were found, leaf chewer, sucker, and stem borer insects, whereas the three major orders Coleoptera, Lepidoptera, and Hemiptera were present along with Orthoptera. The relative abundance of species and the occurrence of families in each guild varied between our results and those found in other studies around the world, but most prominent families in the major guild were present in our results.

In the leaf chewer guild, Meloidae (Coleoptera) represented 54% of the individuals. *Epicauta adspersa* (Klug) was the most abundant defoliator. This species was present throughout the growing season and caused severe defoliation mainly in the early stage of the crop (January) when it compromised the initial stand of plants. Meloid beetles have been previously reported in amaranth plants displaying similar voracity as *E. adspersa* in Argentina, e.g., *Epicauta leopardina* Haag in Paraguay (Schuester 1987) and *Epicauta cinerea* Föster in *A. hypochondriacus* in Mexico (Pérez-Torres *et al* 2011). *Epicauta atomaria* (Germar, 1821) in turn occurred sporadically at very low densities. The abundance of meloid beetles here observed coincides with previous reports in amaranth plants (Kauffman & Weber 1990, Henderson *et al* 1993, Pérez-Torres *et al* 2011).

Lepidopteran larvae are another important group of defoliators, always observed feeding on leaves. In our samples, *A. similalis* (Guenée, 1854) (Crambidae) was the most abundant species. Larvae of this species produced a fine silk and slight curving of the leaf blade. Besides leaves, it has been indicated that *A. similalis* consumes panicles causing agglomeration of floral structures (Guerrero *et al* 2000), but this type of damage was not observed in our study. Instead, we observed cut floral branches in some plants, but we could not determine whether it was made by *A. similalis* or by *Astylus atromaculatus* Blanch (Coleoptera: Melyridae), another species commonly found in inflorescences. In addition to larval stages, we observed many adults of *A. similalis* on the crop. Pupae of this species on weedy *Amaranthus retrofexus* and all insect stages in *A. cruentus* were previously reported (Stegmaier 1950, Guerrero *et al* 2000), which strongly suggests that this species is able to fully develop in plants of the *Amaranthus* genus. *Spodoptera frugiperda* (Smith) and *Rachiplusia nu* (Guenée) (Noctuidae) were present in a similarly lower density, both of them are well-known pest species in corn and sunflower, and they were previously reported in both crop and weedy amaranth species (Stegmaier 1950, Clarke-Harris *et al* 2004, Guerrero *et al* 2000). The low densities of these species here recorded suggest that amaranth is an alternative but not their preferred food plant in the study region. Similarly, species of grasshoppers *Dichroplus maculipennis* (Blanch) and *Dichroplus elongates* Giglio-Tos were observed sporadically, at densities that produced no significant damages. However, given the polyphagy of these species, it should not be discarded that they may be potential pests for this crop given that several species of acridids were cited feeding on *Amaranthus* worldwide (Baloch *et al* 1981, Stegmaier 1950, Jena *et al* 2000, Pérez-Torres *et al* 2011).

Astylus atromaculatus and weevils of the species *N. verecundus* Hustache and *Pantomorus ruizi* (Brèthes) (Coleoptera: Curculionidae) consumed both panicles and leaves. The present study is the first to mention of *A. atromaculatus* in cultivated amaranth, although these species have been mentioned feeding on the weed *Amaranthus hybridus* (vdM Louw & Myburgh 2000). Weevils were the second largest group of insects after meloid beetles, representing about 22% (n=157) of the leaf chewer guild. Several species of weevils feed heavily on both cultivated and weedy *Amaranthus* (Vasicek *et al* 1998, El-Aydam & Bürki 1997, Louw *et al* 1995), some of them considered as potential agents for biological control of amaranth weeds (Napompeth 1982, Kolaib *et al* 1986). Among the species recorded in adult stage, *N. verecundus* was the dominant one, followed by *Conotrachelus* spp. and *Pantomorus auripes* Hustache. Besides defoliator weevils, two stem borer species, *Conotrachelus cervinus* Hustache and *C. histrio* Boheman, caused significant damages. The first species was previously recorded in Argentina on cultivars of *Amaranthus* but only as leaf feeder (Ves Losada & Covas 1987), without any mention about its stem borer habit. *Conotrachelus histrio*, on the other hand, was identified as an efficient agent for biocontrol of the weed *Amaranthus quitensis* in soybean crops due to the intense drilling that their larvae produce in the plants (Vasicek *et al* 1998). *Conotrachelus histrio* found in plants of *Amaranthus* in Argentina has sometimes been referred to as a synonym of *Conotrachelus coelebs* Boheman; however, these are two different species, confused since 1986 (Dr. Charles O'Brien, personal communication). Within the borer guild, a third species was found: *A. quadriplagiata* Boheman (Coleoptera: Cerambycidae). All borer species found in our study have been previously reported feeding in different species of the genus *Amaranthus* (Bosq 1943, Ves Losada & Covas 1987, Vasicek *et al* 1998, Riquelme *et al* 2013); however, we reported for the first time the three species affecting the same stems. The borer guild damage was very noticeable in February, coinciding with advanced stages of the crop, when about 64% of the plants sampled were damaged. The most affected plant parts were main stems, where we found the greatest number of larvae, and it was continued throughout the rachis of the inflorescence. Surprisingly, only a few studies reported a reduction of grain yield in plants with drilled stems (Phogat *et al* 1994), possibly due to larvae not affecting the vascular part of the plant (Bürki *et al* 1997). However, borer guild causes loss of seeds in amaranth crop by downfall of plants due to the weakening of stems and roots depending on the feeding site, below-ground plant parts, e.g., *Hypolixus* spp., *Baris* cf. *dodoris* Marshall (Louw *et al* 1995), *Lixus camerunus* Klobe (Anno-Nyako *et al* 1991), or above-ground plant parts (stem or panicles) as it happened in our study.

Among sucking insects, the occurrence of the species *Edessa meditabunda* and *Nezara viridula* was occasional, while *C. musiva* (Berg) contributed with almost 99% of all the insects observed. The latter species was recorded from January, and its density increased rapidly in the flowering stage and kept constant until the grain filling stage. All individuals were concentrated on panicles, where they fed on immature seeds and possibly sap of floral branches. According to literature, several species, mostly in Aphididae (aphids) and Cicadellidae (leafhoppers) but also in Coreidae, Lygaeidae, and Miridae, occur in weedy amaranth species (El-Aydam & Bürki 1997, Bürki *et al* 2001). In cultivated amaranths, Miridae, Pentatomidae, and Coreidae are the most frequently found families (El-Aydam & Bürki 1997, Salas-Araiza & Boradonenko 2006, Aragón-García *et al* 2011, Pérez-Torres *et al* 2011). Miridae, mainly species of the genus *Lygus* (*Lygus pratensis* L., *Lygus rugulipennis* Poppius, *L.* spp.), are mentioned in cultivated amaranth (Jena *et al* 2000, Louw & Myburgh 2000, Salas-Araiza & Boradonenko 2006), *Lygus lineolaris* (Palisot de Beauvois) being the typical pest species of amaranth in the North America (Weber *et al* 1988, Olson & Wilson 1990).

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