JOURNAL OF APPLIED ENTOMOLOGY

ORIGINAL CONTRIBUTION

Species diversity and distribution of lepidopteran stem borers in South Africa and Mozambique

J. Moolman¹, J. Van den Berg¹, D. Conlong^{2,3}, D. Cugala⁴, S. Siebert¹ & B. Le Ru^{5,6,7}

1 Unit of Environmental Sciences and Management, North-West University, Potchefstroom, South Africa

2 South Sugarcane Research Institute, Private Bag X02 Mount Edgecombe, South Africa

3 Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X01, Matieland, South Africa

4 Eduardo Mondlane University, Faculty of Agronomy and Forest Engineering, Maputo, Mozambique

5 IRD, UR072, Laboratoire Evolution, Génomes et Spéciation (LEGS), UPR 9034 CNRS, Gif-sur-Yvette Cedex, France

6 ICIPE, Nairobi, Kenya

7 Université Paris-Sud 11, Orsay Cedex, France

Keywords

biodiversity, Mozambique, South Africa, stem borers, wild host plants

Correspondence

J. Van den Berg (corresponding author), Unit of Environmental Sciences and Management, North-West University, Potchefstroom 2520, South Africa.

E-mail: johnnie.vandenberg@nwu.ac.za

Received: July 29, 2013; accepted: August 18, 2013.

doi: 10.1111/jen.12085

Abstract

Country-wide surveys of lepidopteran stem borers in wild host plants were undertaken between 2006 and 2009 in South Africa and 2005 and 2010 in Mozambique. A total of 4438 larvae were collected from 65 wild host plants in South Africa and 1920 larvae from 30 wild host plants in Mozambique. In South Africa and Mozambique, 50 and 39 stem borer species were recovered, respectively, with four new species and two new genera among noctuids. Less than 5% of the total number of species collected are considered to be economically important in Africa. These species were *Busseola fusca* (Fuller) (Noctuidae), *Chilo partellus* (Swinhoe) (Crambidae) and *Sesamia calamistis* Hampson (Noctuidae). Data from this study and others in East Africa on the very low abundance of stem borers in wild host plants question the putative role of wild host plants as reservoir for stem borer pests. One new host plant family (Prioniaceae), as well as 24 and 13 wild hosts from South Africa.

Introduction

Lepidopteran stem borers are major pests of cereal crops in sub-Saharan Africa (Harris and Nwanze 1992; Kfir et al. 2002). Haile and Hofsvang (2001) reported that four species of stem borers infested cultivated crops in East Africa. In Southern Africa, the most important stem borers on maize, sorghum and sugar cane are from the families Noctuidae, Crambidae and Pyralidae. These include *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae), *Chilo partellus* (Swinhoe) (Lepidoptera: Noctuidae) (Van Wyk et al. 2007) and *Eldana saccharina* Walker (Lepidoptera: Pyralidae) (Hearne et al. 1994; Assefa et al. 2008).

In Africa, farmers grow their crops in small plots surrounded by wild host plants, which are often infested by stem borers. These wild host plants are sometimes considered to serve as a reservoir, along with crop residues (hosting diapausing larvae), for stem borer pests during the non-cropping season and to be the source of attacks on crops in the following season (Bowden 1976; Polaszek and Khan 1998). However, Le Ru et al. (2006a) reported that noctuid stem borer crop pests are not abundant on wild hosts compared with wild noctuid species.

During the past 50 years, several surveys have been carried out to catalogue the abundance and diversity of lepidopteran stem borers in East and Southern Africa (Ingram 1958; Nye 1960; Haile and Hofsvang 2001; Seshu Reddy 1998; Mazodze and Conlong 2003; Ong'amo et al. 2006, 2013). During these surveys, 22 lepidopteran stem borer species were recorded from 36 host plant species. These species belonged to Noctuidae (11 species), Pyraloidea (nine species), Tortricidae (one species) and Cossidae (one

species). From these surveys, it was concluded that African stem borer species are generally polyphagous. Recently, Le Ru et al. (2006a,b) carried out an extensive survey in East Africa and showed that stem borer diversity is higher and host plant range more extensive than earlier reported. Huge information gaps prevail regarding the distribution and diversity of lepidopteran stem borers and their host plants in Southern Africa.

Although many stem borer species were described from south-eastern Africa and in particular from South Africa (Hampson 1910; Janse 1939; Krüger 2005), studies on diversity and abundance of stem borers in wild host plants are limited in South Africa and Mozambique (Harris and Nwanze 1992; Mazodze and Conlong 2003; Rebe et al. 2004; Le Ru et al. 2006a). Through extensive surveys, this study attempts to catalogue wild host plants and borers in South Africa and Mozambique and to appraise the diversity and distribution of stem borers in wild habitats surrounding graminaceous crops and the potential role of wild habitats as a reservoir for stem borer pests.

Materials and Methods

Surveys of lepidopterous borers in wild host plants were conducted in South Africa between 2006 and 2009 and in Mozambigue in 2005 and 2010. South Africa is situated in a semi-arid region of Africa and has a mean annual rainfall of 543 mm (Schulze et al. 1997). The rainfall gradient in South Africa increases from west to east (Schulze et al. 1997) and can be as high as 1200 mm per annum along certain areas of the eastern Drakensberg escarpment and low-lying coastal regions. Mozambique has a tropical to subtropical climate. The rainfall gradient in Mozambique increases from the south to the north with a mean annual rainfall of almost 1000 mm (McSweeney et al. 2008). Due to the extensive area covered by this study, localities were situated in a wide range of biomes and rainfall regions. The majority of infested host plants were those with thick stems growing in wetter areas of these countries. These areas were mainly streams, rivers, forests and wetlands (Le Ru et al. 2006b).

Surveys were conducted during the rainy seasons from October to March. Although many potential sites were visited, samples were collected at a total of 192 and 78 localities in South Africa (fig. 1) and Mozambique (fig. 2), respectively. These localities were distributed adjacent to cereal crops, along river banks, streams, forest edges and wetlands. A biased sampling procedure was used to increase the probability of finding stem borers as studies have shown a much lower density of borers in wild host plants than in cultivated crops (Gounou and Schulthess 2004: Le Ru et al. 2006a). At each locality, all possible host plant species belonging to Poaceae, Cyperaceae, Juncaceae and Typhaceae were inspected for symptoms of borer damage such as scarified or dry leaves and shoots (dead hearts), frass or holes bored in stems. Infested plants were cut off and dissected in the field. At each locality, the GPS coordinates were noted as well as altitude. These surveys were conducted in rainfall regions ranging from 200 to 1000 mm per annum in South Africa and 700 to 1800 mm in Mozambique. In South Africa, altitudes of the surveyed sites ranged between 3 and 2530 m a.s.l. and in Mozambique between 8 and 1274 m a.s.l. The time spent examining host plants at each locality depended on the levels of infestation. Recovered larvae were placed in vials containing artificial diet (Onyango and Ochieng'-Odero 1994) and reared until pupation. Pupae were kept separately in plastic vials until the adult or parasitoids emerged. Adult moths were identified to species level (Le Ru B.) and voucher specimens deposited in Museum National d'Histoire Naturelle (MNHN, Paris, France) and in ICIPE Museum (Nairobi, Kenva).

During this study, no plant was given host status until the larvae recovered from it were reared through to adult stage. We consider that a host plant is a plant used for food in natural conditions even if we are not certain that the larvae collected would have completed their development on the plant species they were collected from. Host plants were classified according to family and identified up to species level. Species names follow the system used for flowering plants of sub-Saharan Africa (Klopper et al. 2006). Voucher specimens were deposited in the AP Goossens Herbarium, North-West University, Potchefstroom, South Africa.

Stem borer presence–absence data on host plants were subjected to PRIMER (Clarke and Gorley 2001) to elucidate species turnover and similarity of the species assemblages. This non-metric dimensional scaling (NMDS) analyses represent a data matrix of host plant samples and stem borer species in a visual two-dimensional space, allowing for the assumption that samples clustered closer together resemble similar species composition. The distance between each plot on the derived ordination is therefore an indication of dissimilarity in diversity and is therefore a graphical indication of the species turnover between host plants – the larger the distance, the higher the turnover in species (beta diversity).

The host plants were categorized according to their preferred habitat, and four main types were obtained



Fig. 1 Map of South Africa indicating localities surveyed for stem borers in wild hosts between 2006 and 2009.

from Germishuizen et al. (2006). Plants were considered either as helophytic, hydrophytic or mesophytic. If none of the categories were applicable, a plant was considered as terrestrial. Helophytes were considered hydrophytic plants that survive the harsh winter period as buds, while hydrophytes are adapted to live in water or soil permanently saturated with water. Mesophytes are plants that are not specifically adapted to wet environments, but which are often found in damp places. Terrestrial plants, in this context, refer to plants that are able to live in drier environments – often dry, upper banks of streams and rivers along the riparian/non-riparian interface.

Results

Survey in South Africa during 2006–2009

A total of 4438 larvae belonging to 49 stem borer species were collected from 65 wild host plant species.

Twenty seven of these borer species were noctuids (seven *Acrapex* spp., *Busseola fusca*, three *Conicofrontia* spp., *Manga melanodonta*, two *Pirateolea* spp., two *Sciomesa* spp., eight *Sesamia* spp., *Speia vuteria* and two new genera with one species each (named New genus 10 and 11). Significantly fewer species were collected from other families (Tables 1 and 2). Noctuid larvae represented 83% of the total number of stem borers collected, while Pyraloidea made up 8%, Tortricidae 7% and Cossidae only 2% (Table 3).

From the Noctuidae family, the two new genera as well as *Acrapex* spp., *B. fusca, Conicofrontia* spp. and *M. melanodonta* were recovered only from Poaceae. Schoenobiinae were recovered from Cyperaceae and Typhaceae, and Tortricidae were collected from Poaceae, Cyperaceae, Juncaceae and Typhaceae. Crambidae were only collected from one host plant family namely Poaceae. The following species from other families were only recovered from Poaceae: Cossidae, Phycitinae and Pyralidae. *Pirateolea nola* was recov-



Fig. 2 Map of Mozambique indicating localities surveyed for stem borers in wild host plants in 2005 and 2010.

ered from Poaceae, Cyperaceae, Juncaceae and Prioniaceae, while *Pirateolea piscator* was only recovered from Poaceae and Cyperaceae. Two *Sciomesa* species were collected on Cyperaceae and Typhaceae. *Sesamia* spp. was found on Poaceae, Cyperaceae and Typhaceae, while *Speia vuteria* was only found on Typhaceae. *Eldana saccharina* was recovered only from Cyperaceae.

The wild host plants recorded during these surveys are listed in Table 2. Borer larvae were collected from 65 host plant species of which the Poaceae constituted approximately 55% and Cyperaceae 38%. The Poaceae contributed 36 species, Cyperaceae 25, Juncaceae two and Typhaceae and Prioniaceae one each. Poaceae yielded 63% and Cyperaceae 19% of all larvae collected during this four-year survey.

High borer species diversity was found on *Cymbopo*gon nardus (eight species), Miscanthus capensis (eight species), Cymbopogon sp. (six species), Phragmites australis (five species) and Panicum maximum (five species). Among Cyperaceae, high species diversity was found on Carex acutiformis with five species. Four species were recorded on Cyperus dives, Cyperus fastigiatus and Schoenoplectus corymbosus. One other wild host plant species, Typha capensis, was host to seven species in total and 16% of all the collected larvae. The highest number of monophagous stem borers was found on Cymbopogon spp. and Miscanthus capensis with four

 Table 1 Lepidopteran stem borer diversity and abundance on wild host

 plants in South Africa. Numbers in parentheses refer to number of

 species

Number of localities visited	192
Number of host plant species	65
Plant families	
Poaceae	36
Cyperaceae	25
Juncaceae	2
Typhaceae	1
Prioniaceae	1
Stem borer	Individuals
Stem borers collected	4438
Noctuidae	3686
Busseola fusca*	86
Sesamia calamistis*	29
Crambidae (excluding C. partellus)	157 (3 spp.)
Chilo partellus*	75
Pyralidae (excluding <i>Eldana</i>)	1 (1 sp.)
Eldana saccharina*	9
Tortricidae	299 (5 spp.)
Cossidae	72 (1 sp.)
Phycitinae	41 (4 spp.)

*Economically important stem borer species in South Africa.

Schoenobiinae

species each. The economically important stem borer species in South Africa, *B. fusca, S. calamistis, C. partel-lus* and *E. saccharina,* were recorded from several wild host plant species (Tables 2 and 3). *Busseola fusca* was collected from three host plants in the Poaceae only, namely *Arundo donax, Cymbopogon nardus* and *Sorghum arundinaceum,* and accounted for only 2% of the total number of noctuid larvae. *Sesamia calamistis* was found on seven host plants, six Poaceae and one Cyperaceae, making up <1% of the noctuid larvae collected. *Chilo partellus* was found in five different host plants of the Poaceae and accounted for 21% of the Pyraloidea larvae collected. *Eldana saccharina* was found on two host plants and only from the Cyperaceae (5% of the Pyraloidea).

Survey in Mozambique in 2005 and 2010

A total of 1920 stem borers belonging to 39 species were collected from 30 wild host plant species (Table 4). The Noctuidae was the most species-rich family followed by the Crambidae.

A summary of the number of species collected from each host plant family is given in Table 5. From the Noctuidae family, only *Sesamia jansei* and *Sesamia* nov. sp. 16 were recovered from Cyperaceae and Poaceae/ Typhaceae, respectively. All other Noctuidae species were recovered from Poaceae. The species belonging to Pyraloidea were all recovered from Poaceae except for Schoenobiinae sp. 2 (Cyperaceae) and Schoenobiinae sp. 16 (Typhaceae). Tortricidae species were recovered from Poaceae and Cyperaceae and the two Cossidae species from Poaceae. *Chilo* spp. were collected from 17 wild host plant species and Pyralidae from nine species all belonging to Poaceae. Noctuidae represented 51% of the total number of stem borers collected followed by Pyraloidea with 48%, Tortricidae with 1% and Cossidae with <1%.

A total of 30 wild host plants were recorded during this study (Tables 5 and 6). Poaceae made up 83.3% followed by Cyperaceae 13.3% and Typhaceae 3.3%. Poaceae yielded 97% of all the collected stem borer larvae. Cyperaceae and Typhaceae each yielded only 2% of all the stem borers. The plant species with the highest diversity of stem borers was *Panicum maximum* (Poaceae), which yielded 12 species. Nine borer species were collected from *Pennisetum purpureum* and five species from *Rottboelllia cochinchinensis. Cyperus dives* and *Schoenoplectus corymbosus*, both from the Cyperaceae, yielded only two borer species each (Table 6).

The species known to be economically important in Mozambique made up <9% of the total number of stem borers collected. *Chilo orichalcociliellus* was the most abundant with 99 individuals collected from *Heteropogon contortus, P. maximum* and *P. purpureum* (Poaceae). Eighty six individuals of *C. partellus* were collected from five species of Poaceae. Only two individuals of *S. calamistis* were collected from sugar cane. No *B. fusca* was recovered from wild host plants in Mozambique.

Beta diversity patterns

98 (6 spp.)

The species turnover of stem borer species between host plants and habitat types was assessed with NMDS. A first ordination (stress: 0.01) showed an artificial grouping of the majority of the plants into a single cluster (fig. 3a), because three grass and one sedge species played host to only one stem borer species each and were regarded as outliers. These were Phycitinae sp. 19 found only on *Hyparrhenia diplandra*, *Acrapex* sp. 16 found on *Imperata cylindrica* and *Acrapex* sp. 22 collected from an unknown grass species and Schoenobiinae sp. 23 on *Pycreus nitidus*.

A second ordination (stress: 0.09), with the four outliers excluded, indicated no clusters (fig. 3b). This suggests similar stem borer species composition for host plants occurring in similar habitat types. There were no specific stem borer assemblages that charac-

1 1 2 1 2	x x
x x	x x
	x x x x x

*First records of wild host plants for South Africa.

†First records of wild host plants for Africa.

Table 2 (continued)

terized helophytic, mesophytic or hydrophytic host plants. However, if the evolutionary lineages of the host plants are plotted, a clear separation becomes evident between the species assemblages of host plants of the Juncales and Poales (fig. 4).

Discussion

Because the surveys in South Africa were carried out in the central, northern and eastern parts of South Africa, it may underestimate the diversity of stem borers in the western part, which is known to be very dry. Although this part of South Africa often receives <300 mm of rain per annum, the probability of stem borers being present in some areas, especially wetlands, should not be excluded.

Despite several taxonomic studies carried out in the past on stem borers (Hampson 1910; Janse 1939; Krüger 2005), numerous new stem borer species were collected during this study. Several of these species, Manga fuliginosa, Pirateolea nola, Carelis australis, Sesamia pennipuncta, were only recently described (Moyal and Le Ru 2006; Moyal et al. 2010, 2011). Several species are also yet to be described from South Africa. These include Sesamia nov. sp. 4, 12 and 16, Conicofrontia nov sp. 1 and New Genus 10 and 11. In Mozambique, Sesamia nov. sp. 8 and 16 are yet to be described. Many noctuid species recorded during these surveys were not previously collected on their host plants. Pirateolea nola was the borer species with the widest host plant range and was collected from 21 of the 65 plant species (Table 2). This is a much wider host range than the four host species previously reported by Moyal et al. (2010) and indicates how information is rapidly expanded with surveys such as these. In Mozambique, the crambid stem borer species, Chilo sp., infested 16 of the 30 wild host plants.

In the past, extensive surveys have been carried out only on the economical important stem borers, B. fusca, C. partellus and E. saccharina, mainly in cultivated crops (Atkinson 1980; Kfir 1992; Conlong 1997a, 2000; Polaszek and Khan 1998). This study reports for the first time on several stem borer species that are known as pests but of which no knowledge exists outside of cropping systems. Stem borers and their associated parasitoids have been reported to find refuge in wild hosts bordering cultivated crops (Polaszek and Khan 1998). This study indicated that economically important borer species such as B. fusca, B. phaia and C. partellus were not abundant in wild host plants compared with non-pest species. Similar findings were reported by Le Ru et al. (2006a,b) in East Africa.

Busseola phaia was commonly found on wild host species in Mozambique. Although not yet reported from maize in Mozambique or any other country in Southern Africa, most probably because of lack of extensive surveys, it is a potential pest of maize. In fact, this species was common in maize fields in highaltitude areas in Central (Uzungwa Mountain Range near Iringa) and south-western Tanzania (Kipengere Mountain Range near Njombe), where it was present in high infestation levels and caused economically important damage. In fact, this species was more frequently found than B. fusca (Le Ru, unpublished results). Like for *B. segeta* and *P. piscator*, recently reported as new pests of maize in Kenya (Le Ru et al. 2006a), several possibilities may be put forward to explain the reasons for B. phaia establishment in Tanzanian maize fields. These possibilities include the following: (i) this species may have been common in crop fields but remained unknown due to lack of regular stem borer biodiversity surveys in the area, (ii) previously collected material may have been misidentified, and (iii) this species may have expanded its host range to include easily available and more nutritious cultivated crops (maize and sorghum) in response to habitat modification. For example, E. saccharina has shifted hosts from wetland sedges, Cyperus spp., to sugarcane in South Africa (Conlong 1997b), while B. fusca and C. partellus, both wellknown maize stem borers, on sugarcane in Ethiopia (Assefa et al. 2010).

Until recently, it was suggested that larval and pupal stem borer parasitoids can survive the off season and increase their numbers in natural habitats (Khan et al. 1997, Schulthess et al. 1997, Bonhof et al. 2001, Ndemah et al. 2007; Muturi et al. 2005). These authors argued that wild host plants adjacent to cultivated crops provide important refugia for pests. Our study suggests that the stability of the stem borer-parasitoid system during the off season, when crops are not present, is most probably due to persistence of a much diversified stem borer community in the wild habitats, with a small impact on pests. Parasitism of stem borers during the off season was previously thought to occur mainly in natural habitats but (Moolman et al. 2012) showed that although natural habitats provided refuges for some parasitoid species, stem borer parasitism was generally low in wild host plants.

Little information was previously available on stem borer wild host plants in South Africa. Records from earlier studies in South Africa (Pinhey 1975; Atkinson 1980; Kroon 1999) indicated only 24 wild host plants of stem borers in South Africa (Table 7). This study

Table 3	3 Lepidoptera stem	borer abundance per h	lost plant famil	y in South Africa.	Numbers in	parentheses refer to	number of borer species
						1	

	Poaceae	Cyperaceae	Juncaceae	Typhaceae	Prioniaceae	Total
Noctuidae						
Acrapex	237 (7)					237 (7)
Busseola	86 (1)					86 (1)
Conicofrontia	533 (3)					533 (3)
Manga	385 (1)					385 (1)
New Genus 10 nov. sp. 1	24 (1)					24 (1)
New Genus 11 nov. sp. 1	33 (1)					33 (1)
Pirateolea	189 (2)	160 (2)	10 (1)		6 (1)	365 (2)
Sciomesa		238 (2)		21 (1)		259 (2)
Sesamia	1046 (8)	145 (3)		554 (2)		1745 (8)
Speia				19 (1)		19 (1)
Total	2533 (24)	543 (7)	10 (1)	594 (4)	6 (1)	3686 (27)
Pyraloidea						
Crambidae	48 (3)					48 (3)
Chilo sp.	109 (1)					109 (1)
Chilo partellus	75 (1)					75 (1)
Eldana saccharina		9 (1)				9 (1)
Phycitinae	41 (4)					41 (4)
Pyralidae	1 (1)					1 (1)
Schoenobiinae		47 (5)		51 (2)		98 (6)
Total	274 (10)	56 (6)		51 (2)		381 (17)
Tortricidae	9 (1)	276 (2)	12 (1)	2 (1)		299 (5)
Cossidae	72 (1)					72 (1)
Total	81 (2)	276 (2)	12 (1)	2 (1)		4438

 Table 4 Lepidopteran stem borer diversity and abundance in wild host plants in Mozambique

Table 5 Lepidopteran	stem borer abundance	e per host plant family in
Mozambigue. Number	in parentheses refers to	number of species

Cyperaceae

Typhaceae

Total

132 (1)

18 (1)

357 (3)

11 (1)

Poaceae

132 (1)

18 (1)

357 (3)

11 (1)

Noctuidae

Busseola

Carelis

Manga

Pirateolea

78
30
25
4
1
Numbers
1920
840 (11 spp.)
100
152
2 2020 (5)
388 (5 spp.)
99
68
185 (9 spp.)
18 (2 spp.)
2 (2 spp.)
167 (4 spp.)
19 (2 spp.)

Sesamia 425 (6) 20 (1) 456 (7) 11 (2) Total 943 (12) 11 (2) 20 (1) 974 (13) Pyraloidea Crambidae 555 (7) 555 (7) Phycitinae 167 (4) 167 (4) Pyralidae 185 (9) 185 (9) Schoenobiinae 6 (1) 13 (1) 19 (2) 907 (20) Total 6 (1) 13 (1) 926 (22) Tortricidae 1 (1) 17 (1) 18 (2) Cossidae 2 (2) 2 (2) recorded 65 plant species, of which 57 were recorded

*Potentially economically important and reported to attack maize in Kenya.

[†]Economically important stem borers in Mozambique.

recorded 65 plant species, of which 57 were recorded for the first time as hosts of stem borers in South Africa and 13 plant species in Mozambique. These reports increase the list of recorded host plants from 87 (Le Ru et al. 2006b) to 118 species. The number of recorded host plants is sure to increase with more





Fig. 3 Non-metric dimensional scaling (NMDS) of stem borer species on host plants. (a) Clustering is distorted by four outliers. The stress value is below 0.05, which suggests an excellent representation of the data, (b) NMDS of stem borer species and the preferred habitat types of host plants. The four outliers have been removed to visualise the dense, central cluster. The stress value is above 0.05 but <0.1, which suggests that the representation of the data is weak, but interpretable.

such studies undertaken in other areas. For instance, this study has already added a new host plant family, Prioniaceae. The Prioniaceae and the other four known monocotyledonous host plant families are all related and part of the Commelinidae. The Prioniaceae is a monotypic family and is closely related to the Juncaceae within the Juncales (Leistner 2000). *Cymbopogon nardus* and *Panicum maximum*, both belonging to the Poaceae, had the higher species richness in South Africa and Mozambique, respectively. Similar results were reported by Le Ru et al. (2006a,b) in East Africa, with a wider variety of stem borers on Poaceae than that on other wild host plant families.

The ordinations revealed no clear groupings of host plants based on stem borer species assemblages. The high beta diversity (stem borer turnover) suggests that different host plants have their own, unique stem borer assemblages. This host plant specificity is ascribed to the ability of stem borers to recognize the specific leaf surface odours of the preferred host plants (Calatayud et al. 2008; Juma et al. 2013). This specificity is further enhanced by the reduced evolutionary ability of internal plant feeders to colonize new hosts compared with external feeding taxa (Nyman et al. 2006). Despite this specificity, habitat destruction, such diminishing wetlands in the case of *E. saccharina* (Conlong 1997b), may result in host plant switching. Host plant switching is also a common mechanism used by lepidopteran stem borers to survive non-cropping seasons (Ndemah et al. 2007).

Ordinations of the host plant species, based on their habitat preferences, also did not result in clear



Fig. 4 Non-metric dimensional scaling (NMDS) of stem borer species and the lineages of host plants. The four outliers have been removed to visualise the dense, central cluster. The stress value is above 0.05 but <0.1, which suggests that the representation of the data is weak, but interpretable. A star indicates the position of the new host plant genus, Prioniaceae, of the Juncales.

Table 7 List of previously known wild host plants of lepidopteran stem borers from South Africa

	Authority	Stem borer species				
Plant species		Busseola fusca	Chilo partellus	Eldana saccharina	Sesamia calamistis	
Poaceae	(1000)			N.		
Coix lachryma-jobi L.	Atkinson (1980)			X		
Echinocioa stagnina (Retz.)	Atkinson (1980)			Х		
P.Beauv.	Atl					
Paspalum urvillei Steud.	Atkinson (1980)			Х	N/	
Pennisetum sp.	Pinney (1975)	N.			Х	
Saccharum officinarum L.	Kroon (1999)	X		Х		
Sorghum sp.	Kroon (1999)	Х	Х			
Sorghum bicolor (L.)	Atkinson (1980)			Х		
Moench subsp.						
arundinaceum (Desv.) De						
Wet & Harlan						
Triticum vulgare Vill.	Kroon (1999)				Х	
Cyperaceae						
Cladium mariscus (L.) Pohl	Atkinson (1980)			Х		
Cyperus esculentus L.	Atkinson (1980)			Х		
Cyperus fastigiatus Rottb.	Atkinson (1980)			Х		
Cyperus dives Delile	Atkinson (1980)			Х		
Cyperus latifolius Poir.	Atkinson (1980)			Х		
Cyperus natalensis Hochst.	Atkinson (1980)			Х		
ex Krauss						
Cyperus papyrus L.	Kroon (1999)			Х		
Cyperus profiler Lam.	Atkinson (1980)			Х		
Cyperus rotundus L.	Atkinson (1980)			Х		
Cyperus sexangularus Nees	Atkinson (1980)			Х		
Cyperus texilis Thunb.	Atkinson (1980)			Х		
Fuirena umbellata Rottb.	Atkinson (1980)			Х		
Kyllinga elatior Kunth.	Atkinson (1980)			Х		
Cyperus thunbergii Vahl	Atkinson (1980)			Х		
Pycreus polystachyos (Rottb.) P.Beauv.	Atkinson (1980)			Х		

groupings of stem borer assemblages. This suggests that the host, and not the habitat, determines the presence of the stem borer. When the ordination of host plants is considered at a higher taxonomic level (order), a clear separation is evident, which confirms the existence of host specificity between stem borer assemblages and plant orders. Similar assemblages between arthropods and plant orders have been reported for gall midges (Diptera: Cecidomyiidae). Stireman et al. (2010) showed that cecidomyiids radiated in association with the daisies (Asteraceae) and even exhibit strong association with specific evolutionary lineages. Studies conducted on African seed beetles (Coleoptera: Bruchidae) that utilize the family Fabaceae as host plants also indicated that phylogenetically related insects are associated with phylogenetically related host plants, but the phylogeny of the hosts cannot alone explain the observed patterns (Kergoat et al. 2005).

Although the Poales and Juncales share similar habitat types (Siebert et al. 2011), our data suggest that these two phylogenetic lines each tend to be characterized by broad, but specific, assemblages of stem borers that are independent of habitat. The high beta diversity (stem borer turnover) within each order could possibly be ascribed to climatic variation (e.g. tropical Mozambique vs. temperate South Africa) rather than local-scale habitat conditions. In some instances, within a specific climate, the stem borer beta diversity between certain taxa of the Poales and Juncales is indeed small. This was, however, not a new observation because the majority of host plant shifts of arthropods that are internal feeders such as saw flies (Hymenoptera: Tenthredinidae) are known to manifest among phylogenetically close, ecologically proximate hosts (Nyman et al. 2006).

Conclusions

It can be assumed due to wild habitat destruction and fragmentation in response to increasing demands for more agricultural land that future stem borer pests of graminaceous crops will originate from those listed in this study. With regard to the development of integrated pest management strategies, such as habitat management (push–pull) and cultivation of Bt maize, it is essential to understand interactions between stem borer communities in natural and cultivated habitats. These above-mentioned pest management strategies are based on the assumption that stem borer pests prefer to infest wild hosts to cultivated crops. Results presented here clearly question the viability of management methods based on these assumptions.

Acknowledgements

Plant specimens were identified by DR Madeleen Struwig at the AP Goossens herbarium, North-West University and Dr K Gordon-Gray, from the Bews herbarium at the University of Kwa-Zulu/Natal, Pietermaritzburg campus.

References

- Assefa Y, Conlong DE, Van den Berg J, Le Ru BP, 2008. Wider distribution of *Eldana saccharina* Walker (Lepidoptera: Pyralidae) in South Africa and the potential risk to maize production. S. Afr. Sugar Techn. Bull. 81, 290– 297.
- Assefa Y, Conlong DE, Van den Berg J, Mitchell A, 2010. Distribution of sugar cane stem borers and their natural enemies in small-scale farmers' fields, adjacent margins and wetlands of Ethiopia. Int. J. Pest Mana. 56, 233– 241.
- Atkinson PR, 1980. On the biology, distribution and natural host-plants of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). J. Entomol. Soc. South. Afr. 43, 171–194.
- Bonhof MJ, Overholt WA, Van Huis A, Polaszek A, 1997. Natural enemies of cereal stem borers in east Africa: a review. Insect Sci. Appl. 17, 18–35.
- Bowden J, 1976. Stem borer ecology and strategy for control. Ann. Appl. Biol. 84, 107–111.
- Calatayud P-A, Ahuya PO, Wanjoya A, Le Ru B, Silvain JF, Frerot B, 2008. Host plant selection and oviposition behavior of *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae): I-long and short range behaviors. Entomol. Exp. et Applic. 126, 233–243.
- Clarke KR, Gorley RN(2001). PRIMER v.5. User manual/ Tutorial. PRIMER Ltd, Plymouth, UK.
- Conlong DE, 1997a. Biological control of *Eldana saccharina* Walker in South African sugar cane: constrains identified from 15 years of research. Insect Sci. Appl. 17, 69–78.
- Conlong DE, 1997b. Impact of ecology and host plant shifts of *Eldana saccharina* (Lepidoptera: Pyralidae) on its biological control in graminaceous crops. Proc. South Afr. Sugar Techn. Assoc. 71, 94.
- Conlong DE, 2000. Indigenous African parasitoids of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). Proc. South Afr. Sugar Techn. Assoc. 74, 201–211.
- Germishuizen G, Meyer NL, Steenkamp Y, Keith M, 2006. A checklist of South African plants. Southern African Botanical Diversity Network Report No. 41. SABONET, Pretoria, South Africa.
- Gounou S, Schulthess F, 2004. Spatial distribution of lepidopterous stem borers on indigenous host plants in West

Africa and its implications for sampling schemes. Afr. Entomol. 12, 171–178.

Haile A, Hofsvang T, 2001. Survey of lepidopterous stem borer pests of sorghum, maize and pearl millet in Eritrea. Crop Prot. 20, 151–157.

Hampson GF, 1910. Catalogue of the Noctuidae in the Collection of the British Museum. Taylor and Francis, London.

Harris KM, Nwanze KF, 1992. Busseola fusca: a handbook of information. Oxon, UK.

Hearne JW, Van Coller LM, Conlong DE, 1994. Determining strategies for the biological control of a sugar cane stalk borer. Ecol. Model. 73, 117–133.

Ingram WR, 1958. The lepidopterous stalk borers associated with Gramineae in Uganda. Bull. Ent. Res. 49, 367– 383.

Janse AJT, 1939. The moths of South Africa. Cymatophoridae, Callidulidae and Noctuidae (partim). Vol. 3. E. P. and Commercial Printing Co. Ltd, Durban. 307–435.

Juma G, Thiongo M, Dutaur L, Rharrabe K, Marion-Poll F, Le RuB, Magoma G, Silvain J-F, Calatayud P-A, 2013. Two sugar isomers influence host plant acceptance by a cereal caterpillar pest. Bull. Entomol. Res. 102, 20–28.

Kergoat GJ, Delobel A, Fédière G, Le Ru B, Silvain JF, 2005. Both host-plant phylogeny and chemistry have shaped the African seed-beetle radiation. Mol. Phylogenet. Evol. 35, 602–611.

Kfir R, 1992. Seasonal abundance of the stem borer *Chilo partellus* (Lepidoptera: Pyralidae) and its parasites on summer grain crops. J. Econ. Entomol. 85, 518–529.

Kfir R, Overholt WA, Khan ZR, Polaszek A, 2002. Biology and management of economically important Lepidopteran cereal stem borers in Africa. Annu. Rev. Entomol. 47, 701–731.

Khan ZR, Chilishwa P, Ampong-Nyarko K, Smart LE, Polaszek A, Wandera J, Mulaa MA, 1997. Utilization of wild gramineous plants for management of cereal stemborers in Africa. Insect Sci. Appl. 17, 143–150.

Klopper RR, Chatelain C, Bänninger V, Habashi C, Steyn HM, De Wet BC, Arnold TH, Gautier L, Smith GF, Spichiger R, 2006. Checklist of the flowering plants of sub-Saharan Africa. An index of accepted names and synonyms. South African Botanical Diversity Network Report No. 42, 506–508. SABONET, Pretoria.

Kroon DM, 1999. Lepidoptera of Southern Africa – host plants and other associations. A catalogue. Published by the author and Lepidopterists' Society of Africa, Jukskei Park, South Africa.

Krüger M, 2005. New genera and species of noctuid moths from Lesotho (Lepidoptera: Noctuoidea: Noctuidae). Afr. Entomol. 13, 97–142.

Le Ru BP, Ong'amo GO, Moyal P, Ngala L, Musyoka B, Abdullah Z, Cugala D, Defabachew B, Haile TA, Matama-Kauma T, Lada VY, Negassi B, Pallangyo K, Ravolonandrianina J, Sidumo A, Omwega CO, Schulthess F, Calatayud PA, Silvain JF, 2006a. Diversity of lepidopteran stem borers on monocotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. Bull. Entomol. Res. 96, 555–563.

Le Ru BP, Ong'amo GO, Moyal P, Muchugu E, Ngala L, Musyoka B, Abdullah Z, Matama-Kauma T, Lada VY, Negassi B, Pallangyo K, Omwega CO, Schulthess F, Calatayud PA, Silvain JF, 2006b. Geographic distribution and host plant ranges of East African noctuid stem borers. Ann. Soc. Entomol. Fr. 42, 353–362.

Leistner OA, 2000. Seed plants of southern Africa: families and genera. Strelitzia 10, 728–729.

Mazodze R, Conlong DE, 2003. *Eldana saccharina* (Lepidoptera: Pyralidae) in sugarcane (*Saccharum* hybrids), sedges (*Cyperus digitatus*) and bulrush (*Typha latifolia*) in southeastern Zimbabwe. Proc. S. Afr. Sugar Techn. Assoc. 77, 266–274.

McSweeney C, New M, Lizcano G, 2008. UNDP climate change profiles: Mozambique. http://country-profiles. geog.ox.ac.uk. [accessed on 02 September 2013].

Moolman HJ, Van den Berg J, Conlong DE, Cugala D, Siebert SJ, Le Ru BP, 2012. Diversity of stem borer parasitoids and their associated wild host plants in South Africa and Mozambique. Phytoparasitica 41, 89–104.

Moyal P, Le Ru B, 2006. From population to species: morphological and molecular diversity in East African stem borer species of the genus *Manga* Bowden (Lepidoptera: Noctuidae). Ann. Soc. Entomol. Fr. 42, 293–307.

Moyal P, Le Ru B, Conlong D, Cugala D, Defabachew B, Matama-Kauma T, Pallangyo B, Van den Berg J, 2010. Systematics and molecular phylogeny of two African stem borer genera, *Sciomesa* Tams and Bowden and *Carelis* Bowden (Lepidoptera: Noctuidae). Bull. Entomol. Res. 100, 641–659.

Moyal P, Le Ru B, Van den Berg J, Ratnadas A, Cugala D, Matama-Kauma T, Pallangyo B, Conlong D, Defabachew B, 2011. Morphological reinforcement, ancient introgressive hybridization and species delimitation in African stem-borer species of the genus *Sesamia* Guenée (Lepidoptera: Noctuidae). Syst. Entomol. 36, 421–434.

Muturi JJ, Ngi-Song AJ, Schulthess F, Mueke JM, Setamou M, 2005. Location of stem borer pupae in various host plants and implications for the performance of natural enemies with emphasis on pupal parasitoid *Xanthopimpla stemmator* (Hymenoptera: Ichneumonidae). Int. J. Trop. Inst. Sci. 25, 12–18.

Ndemah R, Schulthess F, Le Ru B, Bame I, 2007. Lepidopteran cereal stem borers and associated natural enemies on maize and wild grass hosts in Cameroon. J. Appl. Entomol. 131, 658–668.

Nye IWR, 1960. The insect pests of graminaceous crops in East Africa. Col. Res. Stud. 31, 1–48.

Nyman T, Farrell BD, Zinovjev AG, Vikberg V, 2006. Larval habits, host-plant associations, and speciation in nematine sawflies (Hymenoptera: Tenthredinidae). Evolution 60, 1622–1637.

Ong'amo GO, Le Ru B, Dupas S, Moyal P, Muchugu E, Calatayud PA, Silvain JF, 2006. The role of wild host plants in the abundance of lepidopteran stem borers along altitude gradient in Kenya. Ann. Soc. Entomol. Fr. 42, 363– 370.

Ong'amo GO, Le Ru B, Calatayud P-A, Ogol CKPO, Silvain J-F, 2013. Composition of stem borer communities in selected vegetation mosaics in Kenya. Arthropod Plant Interact. 7, 267–275.

Onyango FO, Ochieng'-Odero JPR, 1994. Continuous rearing of the maize stem borer *Busseola fusca* on an artificial diet. Entomol. Exp. Appl. 73, 139–144.

Pinhey ECG, 1975. Moths of southern Africa. Tafelberg, Cape Town.

Polaszek A, Khan ZR, 1998. Host plants. In: African stem borers; economic importance, taxonomy, natural enemies and control. Ed. by Polaszek A, CTA/CABI. Wallingford, UK, 3–10.

Rebe M, Van den Berg J, McGeogh MA, 2004. Colonization of cultivated and wild graminaceous host plants by *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) under field conditions. Afr. Entomol. 12, 187–199. Schulthess F, Bosque-Perez NA, Chabi-Olaye A, Gounou S, Ndemah R, Goergen G, 1997. Exchange of natural enemies of lepidopteran cereal stem borers between African regions. Insect Sci. Appl. 17, 97– 108.

Schulze RE, Maharaj M, Lynch SD, Howe BJ, Mevil-Thomson B, 1997. South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria.

Seshu Reddy KV, 1998. Maize and sorghum: East Africa. In: African stem borers; economic importance, taxonomy, natural enemies and control. Ed. by Polaszek A. CTA/CABI, Wallingford, UK, 25–28.

Siebert SJ, Siebert F, Du Toit M, 2011. The extended occurrence of Maputaland Woody Grassland further south in KwaZulu-Natal, South Africa. Bothalia 41, 341–350.

Stireman JO, Devlin H, Carr TG, Abbot P, 2010. Evolutionary diversification of the gall midge genus *Asteromyia* (Cecidomyiidae) in a multitrophic ecological context. Mol. Phylogenet. Evol. 54, 194–210.

Van Wyk A, Van den Berg J, Van Hamburg H, 2007. Selection of non-target Lepidoptera species for ecological risk assessment of Bt maize in South Africa. Afr. Entomol. 15, 356–366.