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Host plants and habitats of *Helicoverpa punctigera* and *H. armigera* (Lepidoptera: Noctuidae) in inland Australia

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Abstract For *Helicoverpa punctigera* (Wallengren), and to a lesser extent *Helicoverpa armigera* (Hübner), native host plants in non-cropping regions of inland Australia are believed to be contributors to populations which migrate in spring to infest cropping regions of south-east Australia, and southwestern Australia. Non-crop hosts were sampled using sweep nets in 71 survey trips in 19 years between 1987 and 2017 for larvae of *H. punctigera* and *H. armigera*, over about 2.4 million km^2 in inland Australia. Of 1976 samples, *H. punctigera* larvae were present in 50.5%, distributed throughout the study area. Larvae were found on 106 host plant species in 24 families, including 61 new host records. *H. armigera* larvae were found on 33 plant species from eight families, including 14 new host records. However, only 4.3% of samples were positive for this species, and they were mostly in the east of the study area and had fewer larvae than the positive *H. punctigera* samples. *H. punctigera* larvae were found in each of six habitats, being, in order of mean numbers per sample: sandy deserts > floodplains > mulga, grasslands and saltbush > stony downs. Host status was determined for both species by plotting relative incidence against relative abundance, and the good hosts for *H. punctigera* differed between habitats. We discuss the value and limitations of this approach for identifying key hosts in broad scale population dynamics, and primary hosts which may have close co-evolutionary histories with the insects.

Key words *Helicoverpa armigera*, *Helicoverpa punctigera*, habitats, host plants, inland Australia, migration.

INTRODUCTION

The larvae of moths in the subfamily Heliothinae affect many crops around the world (Sharma 2005). In Australia, *Helicoverpa punctigera* (Wallengren) and *Helicoverpa armigera* (Hübner) are significant pests of cotton, oilseeds, grain legumes, vegetables and (for *H. armigera* only) corn and sorghum (Zalucki *et al*. 1986; Fitt 1989). *Helicoverpa armigera* is cosmopolitan, including recent incursions to South and North America (Kriticos *et al*. 2015). *Helicoverpa punctigera* is endemic to Australia, and its distribution is restricted to the Australasian region (Matthews 1999). Both species are highly polyphagous (Zalucki *et al*. 1986; Zalucki *et al*. 1994; Cunningham & Zalucki 2014) and highly migratory (Daly & Gregg 1985; Farrow & Daly 1987; Gregg 1995).

For *H. punctigera*, native host plants in non-cropping regions of inland Australia are believed to be key contributors to populations which migrate in spring to infest cropping regions of south-east Australia (Gregg *et al*. 1993, 1995, 2001) and southwestern Australia (Walden 1995). Rainfall, especially in autumn and winter, determines the extent of these hosts and the size of spring immigrations can sometimes be correlated with inland rainfall (Oertel *et al*. 1999, but see also Baker *et al*. 2011).

Zalucki *et al*. (1994) described host plants recorded in north-western New South Wales and western Queensland between 1987 and 1990. A total of 554 sweep net samples were made at 401 sites, on 96 potential host plants. *H. punctigera* larvae were recovered from 47 plant species of which 45 were new host records. For *H. armigera*, larvae were recovered from 28 plant species, of which 25 were new host records. We add to these records new data from inland surveys conducted from 1991 to 1994, in 1997, 2000, and from 2009 to 2017. The range of sampling is extended to the south and west of the original study area, and data from an additional 1413 sweep net samples are included.

Zalucki *et al*. (1994) introduced the concept of assessing host status using a matrix of relative abundance plotted against relative incidence (Fig. 1). Here, we critically evaluate this approach, and apply it to identify important host plants in six distinct habitats for *H. punctigera* in inland Australia. We assess the importance of each of these habitats in the continental-scale population dynamics of *H. punctigera*. The data from Zalucki *et al*. (1994) are included in these analyses for completeness.

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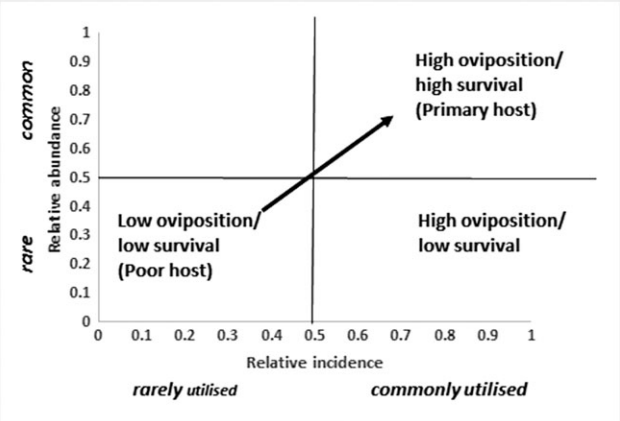

Fig. 1. Matrix for host plant status, after Zalucki *et al.* (1994). Relative incidence is the proportion of samples positive, relative to the most frequently utilised host. Relative abundance is the mean number of larvae per sample (positive samples only), relative to the host with the highest mean numbers.

MATERIALS AND METHODS

Study area and survey trips

The study area consisted of approximately 2.4 million km^2 in inland Australia, encompassing western parts of New South Wales and Queensland, northern parts of South Australia, southern parts of the Northern Territory and eastern parts of Western Australia (Fig. 2). This region has almost no crops, and the vegetation is dominated by native species. The area is arid or semi-arid, and rainfall is extremely variable (Morton *et al.* 2011). While there is a tendency for summer rainfall to be more prevalent in the north and winter rainfall in the south substantial falls can occur at any time, though many months or even years can pass between significant falls in some areas.

We identified six broad vegetation/landform classifications ('habitats'; Fig. 2), drawing on those described by Morton *et al.* (2011): (1) sandy deserts, including sand dune/clay pan systems and spinifex plains; (2) floodplains, riparian areas subject to irregular inundation that were at least 500 m wide, smaller inundated areas being described as creek lines and samples from them allocated to the habitat in which they occurred; (3) mulga (*Acacia* shrublands), dominated by trees or tall shrubs in the genus *Acacia*; (4) grasslands, sparsely timbered habitats dominated by grasses; (5) saltbush (chenopod shrublands), dominated by chenopods especially *Atriplex* spp. and *Maireana* spp.; and (6) stony downs, flat to undulating habitats characterised by large areas of bare rock with patches of short grasses, succulents and chenopods.

Regions in which the six habitats were most commonly found are shown in Figure 2, but in many areas, there was a fine-grained mosaic of different habitats. Sandy deserts were mostly located in the centre and west of the study area and included the Simpson and Great Victoria deserts. They

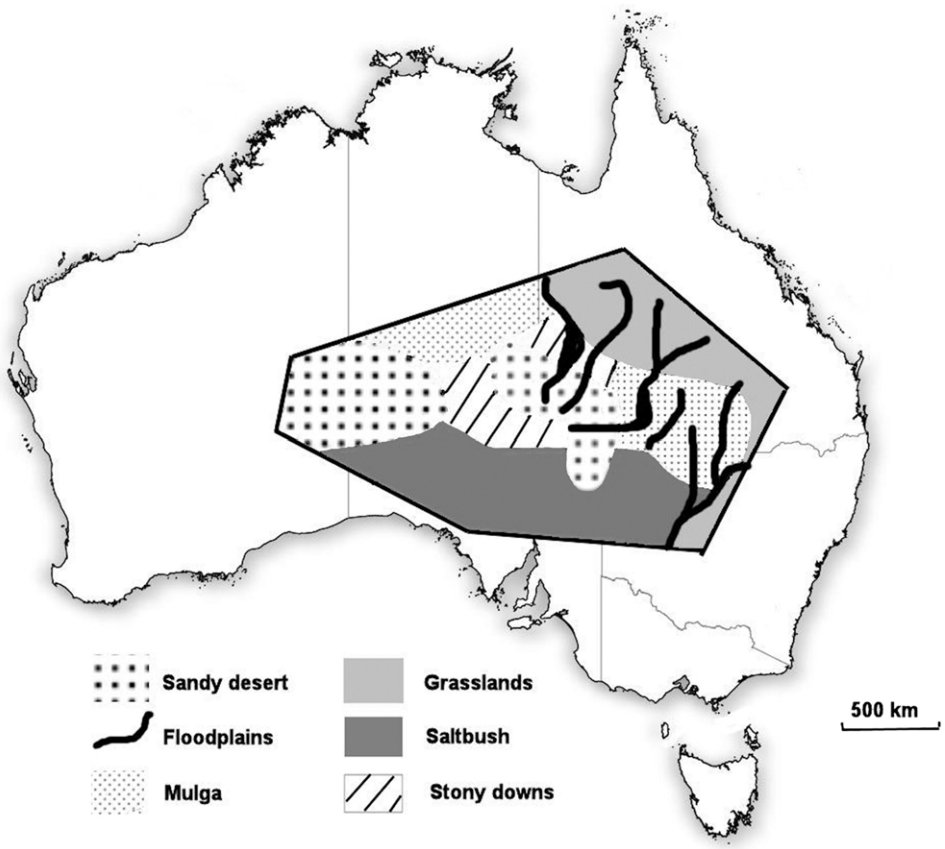

Fig. 2. Study area showing regions in which the six habitats were most commonly found.

supported host plants both on the dunes and in clay pans between dunes. The dominant vegetation was usually spinifex grasses (*Triodia* spp.) along with *Acacia* spp. and other perennial shrubs. Floodplains, occupying the smallest area of any habitat, were located in the eastern and central regions. They were dominated by grasses and legumes, and included the Darling, Paroo, Warrego and Bulloo Rivers, which drain to the Murray–Darling basin in the east. These eastern floodplains were usually narrower than those of the Diamantina River and the Barcoo–Thomson–Cooper and Eyre–Georgina systems, which drain internally to the Lake Eyre basin in the centre. Mulga habitats were located mostly in the east and northwest, with only scattered patches in the centre. They were dominated by *Acacia* spp., often but not always mulga (*A. aneura* F. Muell. ex Benth.), and supported a diverse range of hosts between and under the *Acacia* shrubs. Grasslands were most extensive in the northeast of the study area (the Mitchell grass plains of central and western Queensland, dominated by *Astrebla* spp.), but patches dominated by other grass species occurred elsewhere. Stony downs were undulating to flat areas found mostly in central regions, often forming a mosaic with sandy deserts and mulga. They supported mostly short grasses, succulents and perennial chenopods. While chenopods were common in most habitats, they dominated the plains in the southern parts of the study area, western New South Wales and South Australia, making up the saltbush habitat, with *Medicago* spp. and daisies between the shrubs.

A total of 71 survey trips were made to the study area, involving a total of 2073 samples (Table 1). Trips usually targeted an area where recent rain had fallen, but these areas were often small and to reach them large areas of dry habitats were traversed. Of the 2073 samples, 106 were made in cropping regions on the southern and eastern margins of the study area, and these have been omitted from the analyses reported here. Most trips were made between March and November, with only two (1991 and 1993) in January, and none in February.

Table 1 Number of field trips and samples in each year of the study

Year	Number of trips	Samples
1987	2	15
1988	4	112
1989	4	195
1990	12	321
1991	9	371
1992	4	168
1993	6	172
1994	3	92
1997	1	52
2000	3	166
2009	2	29
2010	2	65
2011	2	34
2012	2	29
2013	1	7
2014	3	29
2015	3	63
2016	6	108
2017	2	45
Total	71	2073

Sampling methods

Sweep net sampling as described by Zalucki *et al*. (1994) was used. On each field trip, roads and tracks in inland regions were traversed and when a patch or patches of potential hosts suitable for sweep netting (total area >150 m^2 and pure enough to avoid contamination of samples by larvae from intermingled plants), 100 or 200 sweeps were made in replicates of 20 sweeps with a 38 cm net. On a few occasions when host patches were small, fewer sets of 20 sweeps were made.

The latitude and longitude of the sample sites was recorded using GPS from 1993, and for earlier trips by vehicle odometer readings from known locations. Sites were allocated to one of the six habitat classifications with the aid of digital georeferenced vegetation maps published by various State authorities. For example in New South Wales, we used the Vegetation Classes of NSW map (Keith & Simpson 2012). A sample of larvae (at least 12, or all those collected if the total catch was less than 12) was reared on artificial diet (Teakle & Jensen 1991) to confirm identification. Larval densities were calculated by multiplying the total catch per 100 sweeps by the proportion of surviving larvae which were identified as *H. punctigera* or *H. armigera*. Where there was doubt about the identity of the host plant, samples were pressed and submitted to the Queensland Herbarium or the herbaria of CSIRO or the University of New England for identification. Only partial plant identifications (to genus or family) were obtained for 136 samples. These have been included for calculating overall incidence and mean numbers of positive samples in each habitat, but omitted from the host status analyses described here, along with the 106 samples from cropping regions.

Determination of host plant status from survey data

We used the matrix of Zalucki *et al*. (1994) to assess the status of host plants which were sampled six times or more. The relative incidence of larvae on these plants was calculated as the proportion of samples that were positive for *H. punctigera* larvae on that plant, divided by the proportion positive for the reference host. The reference host was the plant which had the highest proportion of samples that were positive. It was interpreted as a measure of how well host plant patches are found and utilised. The relative abundance was found by dividing the mean number of larvae per 100 sweeps (positive samples only) for a plant species by the corresponding value for the reference host (the plant with the highest mean number of larvae). This was interpreted as indicating suitability for oviposition and larval survival. These relative measures (ranging from 0 to 1) were plotted on a graph divided into four quadrants which indicated the status of the host plant (Fig. 1). Here, we avoid the use of 'primary host' (Zalucki *et al*. 1994) and consider the top two quadrants to include 'good' hosts, the bottom right quadrant to include 'fair' hosts and the bottom left to include 'poor' hosts.

RESULTS

Distribution of positive and negative samples

For *H. punctigera*, from 1967 samples (after omitting those from cropping regions), 992 were positive (50.5%). The positive samples were distributed throughout the study area. Numbers of larvae often exceeded 10, and sometimes exceeded 100, per 100 sweeps (Fig. 3). For *H. armigera*, again omitting cropping regions, there were 85 positive samples (4.3%). The positive samples were mostly in the north-east of the study area, and generally had fewer than 10 larvae per 100 sweeps (Fig. 4).

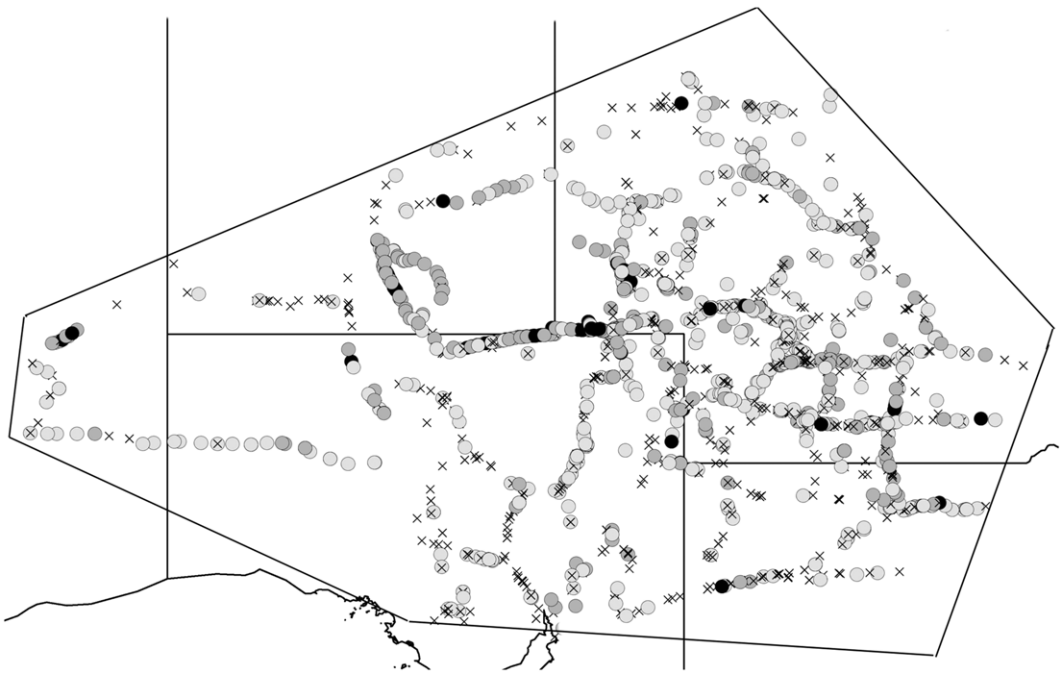

Fig. 3. Distribution of positive and negative samples for *H. punctigera*. x = negative sample, ● = 1–10 larvae per 100 sweeps, ● = 10–100 larvae per 100 sweeps, ● = >100 larvae per 100 sweeps.

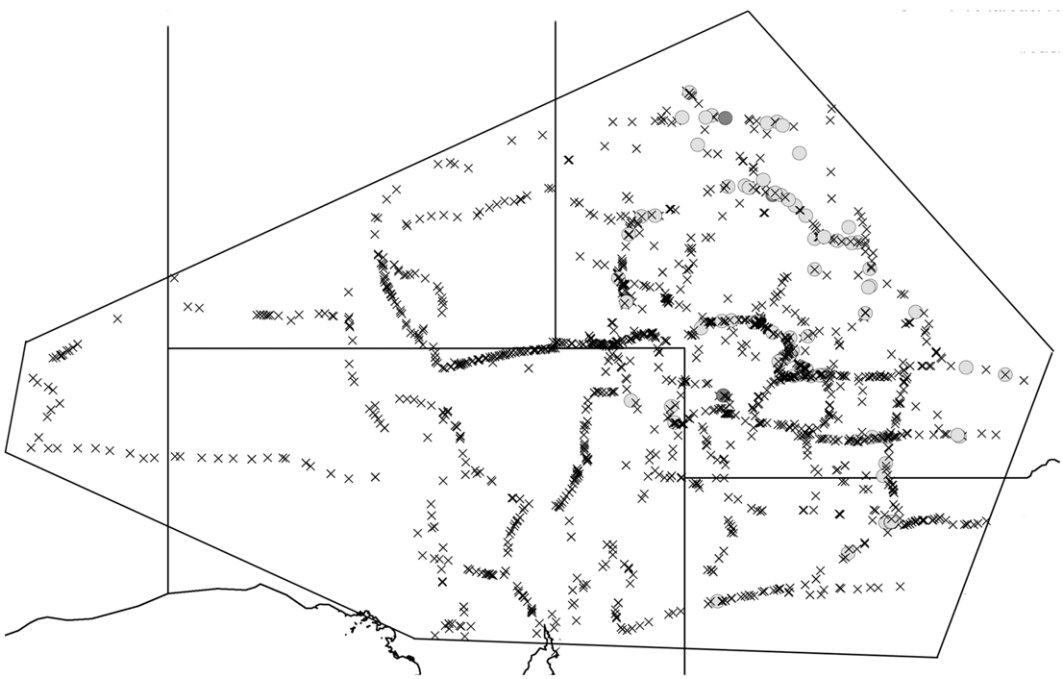

Fig. 4. Distribution of positive and negative samples for *H. armigera*. x = negative sample, ● = 1–10 larvae per 100 sweeps, ● = 10–100 larvae per 100 sweeps.

Host plant status

For *H. punctigera*, larvae were recorded on 106 plants in 24 families (Table 2). Of these, 61 are new host records, i.e. they were not sampled by Zalucki *et al*. (1994) or were sampled then with negative results. Nor have they been recorded as hosts by other authors. *H. armigera* larvae were found on 33 host plants from eight families (Table 3). Of these, 14 are new host records.

There were 102 plant taxa (including a few only identified to genus) that yielded no larvae of either species. Many were sampled only once or twice, usually reflecting the rarity of stands suitable for sweep netting. A list of these follows, with the number of samples in parentheses and genera for which larvae were recorded on other species (Tables 2 and 3) prefaced by an asterisk:

Aizoaceae: *Glinus lotioides* L. (1), *Disphyma crassifolium* (L.) L. Bolus. (1); Amaranthaceae: **Ptilotus nobilis* (Lindl.) F. Muell. (2),**Ptilotus latifolius* R.Br. (1), **Ptilotus seminudus* (J. M. Black) J.M. Black (1) **Ptilotus obovatus* (Gaudich.) F. Muell. (2), **Ptilotus sessifolius* (Lindl.) Benl (2); Apiaceae: *Eryngium plantaginaeum* F. Muell. (2). Araliaceae: *Trachymene glaucifolia* (F. Muell.) Benth. (4). Asphelodelaceae: *Asphodelus fistulosis* L. (1); Asteraceae*: *Brachyscome goniocarpa* F. Muell. (1), *Calocephalus platycephalus* (F. Muell.) Benth. (1), **Calotis porphyroglossa* F. Muell ex Benth. (1), **Chrysocephalum erimaeum* (Haegi) Anderb. (1), **Chrysocephalum pterochaeum* F. Muell. (1), **Craspedia uniflora* G. Forst. (1), *Ethuliopsis cunninghamii* (Hook.) F. Muell. (2), *Erodiophyllum elderi* F. Muell (1), **Gnephosis eriocarpa* (F. Muell.) Benth. (1), *Ixioclamys integerrima* Dunlop (1), **Minuria cunninghamii* (DC.) Benth. (1), *Oncosiphon suffruticosum* (L.) Kallersjo (1), **Pterocaulum serrulatum* (Montrouz.) Guillaumin (1), **Pycnosorus eremaeus* J. Everett & Doust (1), *Reichardia tingitana* (L.) Roth (1), **Senecio glossanthus* (Sond.) Belcher (1), *Tricanthodium skirrophorum* Sond. & F. Muell. Ex Sond. (1), *Vittadinia sulcata* N.T. Burb. (1). Boraginaceae: *Heliotropium amplexicaule* Vahl (2), *Trichodesma zeylanicum* (Burm. f.) R.Br. (6), *Zygophyllum auranticum* (Lindl.) F. Muell. (1); Brassicaceae: *Arabidella nasturtium* (F. Muell.) E. A. Shaw (1), *Arabidella trisecta* (F. Muell.) O.E. Schulz (1), *Brassica tournefortii* Gouan (9), *Carrichtera annua* (L.) DC. (18), *Pachymitus cardaminoides* (F. Muell.) O.E. Schulz (1), *Sysimbium eresimoides* Desf. (1), *Sysimbium irio* L. (1), *Stenopetalum nutans* F. Muell. (3); Chenopodiaceae: *Atriplex muelleri* Benth. (4*), Atriplex vesicaria* Heward ex Benth. (7*) Chenopodium auriocomum* Lindl. (3), *Maireana astrotricha* (L.A.S. Johnson) Paul G. Wilson (3), *Maireana pyrimidata* (Benth.) Paul G. Wilson (2), *Maireana sedifolia* (F. Muell.) Paul G. Wilson (5), *Neobassia proceriflora* (F. Muell.) A.J. Scott (1), *Rhagodia parabolica* R.Br. (1), *Sclerolaena articulata* (J.M. Black) A.J. Scott (2), *Sclerolaena cornishiana* A.J. Scott (3), unidentified *Atriplex* spp. (3), unidentified *Sclerolaena* spp. (4), unidentified *Tecticornia* spp. (5); Convolvulaceae: *Polymeria longifolia* Lindl. (1); Cucurbitaceae: *Cucumis myriocarpus* Naudin. (1); Fabaceae: *Acacia victoriae* Benth. (2), **Crotalaria eremaea* F. Muell. (4), **Crotalaria medicaginea* Lam. (1), **Crotalaria montana* K. Heyne ex Roth (1), **Crotalaria smithiana* A.T. Lee (1*), Indigofera linifolia* (L.f.) Retz. (1), *Kennedia prorepens* (F. Muell.) F. Muell. (1), **Medicago trunculata* Gaert (1), *Neptunia monosperma* F. Muell. ex Benth. (1), *Rhyncosia minima* (L.) DC. (2), *Senna artemesioides* (Gaudich. ex DC.) Randell (4), *Stylosanthes hamata* (L.) Taub. (2), **Swainsona galegifolia* (Andrews) R.Br. (1), **Swainsona oroboides* F. Muell. ex Benth. (1), **Swainsona swainsonoides* (Benth.) A.T. Lee ex J.M. Black (1), *Tephrosia brachyodon* Domin. (1); Geraniaceae: **Erodium cygnorum* Nees (1); Goodeniaceae: **Goodenia glabra* R. Br. (1), **Goodenia heteromera* F. Muell. (1), **Goodenia lunata* J.M. Black (2), *Scaevola humilis* R.Br. (1), *Scaevola parviflora* F. Muell. ex Benth. (1); Haloragaceae: *Haloragis glauca* Lindl. (5); Lamiaceae: *Basilicum polystachyon* (L.) Moench (1), *Marrubium vulgare* L. (2), *Salvia verbenaceae* L. (1), *Teucrium racemosum* R.Br. (1), Malvaceae: *Gossypium australe* F. Muell. (7), *Gossypium sturtianum* J.H. Willis (1), *Sida cardiophylla* (F. Muell. Ex Benth.) F. Muell. (1), **Sida cordifolia* L. (2); Marsilaceae: *Marsilea* sp. (3); Oxlidaceae: *Oxalis pes-caprae* L. (6); Plantaginaceae: *Stemodia florulenta* W.R. Barker (2); Poaceae: *Astrebla pectinata* (Lindl.) F. Muell. ex Benth. (6), *Cenchrus ciliaris* L. (1), *Chloris gayana* Kunth. (1), unidentified Poaceae (9); Polygonaceae: *Acetosa vesicaria* (L.) À. Löve (1), *Rumex crispus* L. (1); Scrophulariaceae: *Eremophila longifolia* (R.Br.) F. Muell., (1), *Eremophila gilesii* F. Muell. (3); Solanaceae: **Solanum quadriloculatum* F. Muell. (7); Thymelaceae: *Pimelea decora* Domin. (1), *Pimelea simplex* F. Muell. (3); Zygophyllaceae: *Zygophyllum ovatum* Ewart & Jean White (1), *Tribulus terrestris* L. (1), *Zygophyllum auranticum* (Lindl.) F. Muell. (1).

For *H. punctigera*, across all habitats, there were only three good hosts, all of which were annual Asteraceae and all of which were frequently utilised (Fig. 5a). They were *Polycalymma stuartii*, *Senecio gregorii* and *Rhodanthe charsleyae*. There were many fair hosts, which were frequently utilised but supported fewer larvae than the three daisies on average; these included many other Asteraceae, especially annuals but with a few short-lived perennials (Table 2). There were many hosts in the Fabaceae, especially annuals, and a few plants from other families including Geraniaceae, Goodeniaceae, Malvaceae and Solanaceae as well as many poor hosts (Table 2), including some perennials.

For *H. armigera*, there were also three good hosts, *Apowollastonia cylindrica*, *Sida ammophila* and *Sonchus oleraceae*. There were also two widely utilised hosts that supported fewer larvae, *Senecio platylepis* and *Podolepsis jaceioides*. Of these, all except *S. ammophila* are annual daisies, and all except this species and *S. oleraceus* (which is an introduced weed of disturbed areas) are distributed only in the east of the study area.

Helicoverpa punctigera in different habitats

The proportions of positive samples for *H. punctigera* and the mean numbers per 100 sweeps in those samples in the six habitats are shown in Figure 6. There were insufficient data for a similar analysis with *H. armigera* – most positive samples for this

Table 2 Number of samples, percentage of positive samples, mean numbers per positive sample and putative status of host plants for *H. punctigera*

Host plant	*N* samples	% + ve	Mean ± s.e.	Status
Amaranthaceae				
Ptilotus macrocephalus (R.Br.)Poir	6 (2)	33	1.0 ± 1.0	P
Ptilotus polystachyus (Gaudich.)F. Muell.	19 (3)	26	3.5 ± 0.6	P
Ptilotus sessilifolius (Lindl.) Benth.	2	100	1.5 ± 0.5	U, N
Asteraceae				
Apowollastonia cylindrica Orchard	6 (3)	83	24.7 ± 21.5	F
Brachyscome campylocarpa J.M. Black	1	100	5.0	U, N
Brachyscome ciliaris (Labill.) Less.	9 (1)	44	7.0 ± 2.3	P
Brachyscome ciliocarpa W. Fitzg.	1	100	6.7	U, N
Brachyscome melanocarpa F. Muell.	1 (1)	100	1.5	U
Calendula arvensis L.	1	1	3.0	U, N
Calotis ancyrocarpa J.M. Black	6 (5)	67	14.9 ± 5.0	F
Calotis cuneifolia R.Br.	24 (14)	79	22.8 ± 7.1	F
Calotis erinaceae Steetz	4 (2)	25	1.0	U, N
Calotis hispidula (F. Muell.) F. Muell.	4	50	1.0	U, N
Calotis lappulacae Benth.	4 (1)	75	2.8 ± 1.3	U, N
Calotis latiuscula F. Muell & Tate	6	83	7.5 ± 1.2	F, N
Calotis multicaulis (Turcz.) Druce	49 (28)	59	6.4 ± 1.7	F
Calotis plumulifera F. Muell.	1	100	5.0	U, N
Calotis scabiosifolia Sond. & F. Muell.	2	100	39.8 ± 15.0	U, N
Chrysocephalum apiculatum (Labill.) Steetz	13 (1)	23	6.2 ± 1.2	P, N
Craspedia haplorrhiza J. Everett & Doust	1	100	20.8	U, N
Gnephosis arachnoidea Turcz	13 (1)	38	10.9 ± 6.4	P, N
Hyalosperma semisterile (F. Muell.) Paul G. Wilson	5 (2)	60	4.0 ± 3.0	U, N
Lawrencella davenportii (F. Muell.) Paul G. Wilson	9	44	6.5 ± 4.0	P, N
Leiocarpa brevicompta (F. Muell.) Paul G. Wilson	17 (12)	82	24.0 ± 8.8	F
Leiocarpa leptolepis (DC.) Paul G. Wilson	4	25	2.0	U, N
Leucochrysum molle (A. Cunn. Ex DC.) Paul G. Wilson	25 (6)	60	22.1 ± 12.0	F
Leucochrysum stipitatum (F. Muell.) Paul G. Wilson	2	50	15.0	U, N
Minuria denticulata (DC.) Benth.	8 (3)	63	3.9 ± 2.4	F
Minuria integerrima (DC.) Benth.	6	50	3.8 ± 1.2	F, N
Minuria leptophylla DC.	5 (1)	80	5.8 ± 1.8	U
Olearia pimelioides (DC.) Benth.	1	100	0.5	U, N
Ozothamnus cassinioides (Benth.) Anderb.	1	100	2.0	U, N
Podolepis canescens A. Cunn. Ex DC	4 (3)	75	37.0 ± 25.1	U, N
Podolepis jaceioides (Sims) Voss	8 (8)	50	6.1 ± 1.8	F
Podolepis longipedata A. Cunn. Ex DC	2 (1)	100	6.8 ± 3.3	U, N
Polycalymma stuartii F. Muell. & Sond. Ex Sond.	91 (17)	64	70.9 ± 9.9	G
Pterocaulum sphacelatum (Labill.) F. Muell.)	11 (1)	27	3.1 ± 1.2	P, N
Pycnosorus chrysanthus (Schltdl) Sond.	26 (13)	42	9.2 ± 5.4	P, N
Pycnosorus globosus F.L. Bauer ex Benth.	5 (3)	80	5.9 ± 2.1	U
Pycnosorus pleiocephalus (F. Muell.)J. Everett & Doust	4 (2)	25	2.2 ± 0.3	U
Rhodanthe anthemoides (Seiber ex Spreng.) Paul G. Wilson	1 (1)	100	12.0	U
Rhodanthe charsleyae (F. Muell.) Paul G. Wilson	20	90	57.9 ± 16.4	G, N
Rhodanthe floribunda (A. Cunn. ex DC.) Paul G. Wilson	212 (101)	74	24.0 ± 3.6	F
Rhodanthe microglossa (Maiden & Betche) Paul G. Wilson	4 (2)	100	4.5 ± 2.0	U
Rhodanthe pygmaea (DC.) Paul G. Wilson	1	100	5.0	U, N
Rhodanthe stricta (Lindl.) Paul G. Wilson	41 (27)	63	6.3 ± 1.3	F
Rhodanthe stuartiana (Sond. & F. Muell) Paul G. Wilson	3	100	36.3 ± 25.3	U, N
Rhodanthe tietkensii (F. Muell.) Paul G. Wilson	3	67	11.5 ± 4.5	U, N
Rutidosis helichrysoides DC.	7	29	1.5 ± 0.5	P, N
Schoenia ayersii (F. Muell.) J.M. Black	2	100	10.5 ± 0.5	U, N
Schoenia cassiniana (Gaudich.) Steetz	4	75	14.2 ± 5.2	U, N
Senecio cunninghamii DC.	1 (1)	100	0.5	U
Senecio gregorii F. Muell.	97 (11)	78	59.4 ± 11.6	G
Senecio lautus G. Forst. ex Willd.	32 (12)	47	6.5 ± 1.6	P
Senecio magnificus F. Muell.	12	67	17.6 ± 6.3	F, N
Senecio platylepis DC.	6 (4)	67	7.0 ± 3.3	F
Sonchus oleraceus L.	7 (7)	14	1.0	U
Verbesina encelioides (Cav.) Benth. & Hook. F. ex A. Gray	23 (2)	48	17.0 ± 7.2	P
Waitzia acuminata Steetz	19 (1)	74	4.9 ± 1.1	F, N
Xerochrysum bracteatum (Vent.) Tzvelev	8 (1)	38	17.2 ± 13.2	P

(*Continues*)

Table 2 (Continued)

Host plant	*N* samples	% + ve	Mean ± s.e.	Status
Boragincaceae				
Echium plantagineum L.	28 (13)	64	14.5 ± 4.0	F
Brassicaceae				
Blennodia canescens R.Br.	6 (1)	33	4.0 ± 3.0	P, N
Blennodia pterosperma (J.M. Black) J.M. Black	2 (1)	100	15.0 ±	U
Harmsiodoxa blennodioides (F. Muell.) O.E. Schulz	1	100	2.0	U, N
Harmsiodoxa puberula E.A. Shaw	4 (3)	25	2.5	U
Lepidium phlebopetalum (F. Muell.) F. Muell.	1	100	3.0	U, N
Rapistrum rugosum (L.) All.	2	100	21.6 ± 11.6	U, N
Cleomaceae				
Cleome viscosa L.	3	33	1.0	U, N
Fabaceae				
Aeschynomene indica L.	5	80	9.7 ± 6.3	U, N
Crotalaria dissitiflora Benth.	11	36	1.9 ± 1.4	P, N
Cullen australasicum (Schltdl	21 (6)	48	5.7 ± 1.4	P
Cullen cinereum (Lindl.) J.W. Grimes	325 (17)	57	27.3 ± 5.1	F
Cullen graveolens (Domin.) J.W. Grimes	3	100	6.9 ± 1.4	U, N
Cullen patens (Lindl.) J.W. Grimes	4 (2)	25	2.5	U
Cullen pallidum (Burb.) J.W. Grimes	7	100	24.6 ± 13.1	F, N
Medicago laciniata (L.) Mill.	5 (2)	50	65.8 ± 60.3	U
Medicago polymorpha L.	44 (18)	27	15.8 ± 5.1	P
Sesbania brachycarpa F. Muell.	5	60	4.2 ± 2.4	U, N
Swainsona campylantha F. Muell.	4	75	6.4 ± 1.8	U, N
Swainsona stipularis F. Muell.	5 (1)	40	6.5 ± 5.5	U
Trigonella suavissima Lindl.	14	43	10.4 ± 3.7	P, N
Geraniaceae				
Erodium crinitum Carolin	12 (2)	83	4.7 ± 1.4	F
Goodeniaceae				
Goodenia berardiana (Gaudich.) Carolin	1	100	1.5	U, N
Goodenia cycloptera R.Br.	5	60	27.7 ± 7.1	U, N
Goodenia fascicularis F. Muell. & Tate	6	33	2.2 ± 0.8	P, N
Goodenia glauca F. Muell.	8	63	5.8 ± 2.9	F, N
Velleia glabrata Carolin	66 (46)	64	3.3 ± 0.5	F
Lamiaceae				
Teucrium integrifolium Benth.	2	50	3.0	U, N
Malvaceae				
Abelmoschus ficulneus (L.) Wight	3	33	5.0	U, N
Abutilon otocarpum F. Muell.	11 (1)	9	2.7	P, N
Malva parviflora L.	3	33	14.7	U, N
Malva weinmanniana (Besser ex Rchb.)	5	20	11.0	U, N
Malvastrum americanum (L.) Torr.	41 (4)	20	7.2 ± 2.0	P
Sida ammophila F. Muell. ex J.H. Willis	8 (3)	37	19.2 ± 10.0	P
Sida calyxhymenia J. Gay ex DC.	1	100	1.0	U, N
Sida platycalyx F. Muell. Ex Benth.	23 (2)	9	4.9 ± 0.9	P
Sida trichopoda F. Muell.	8	50	33.7 ± 10.5	F, N
Phyrmaceae				
Mimulus gracilis R. Br.	1	100	12.0	U, N
Plantaginaceae				
Stemodia glabella W.R. Barker	6	33	6.0 ± 5.0	P, N
Poaceae				
Dactyloctenium radulans (R.Br.) P. Beauv.	2	50	2.9	U, N
Amphipogon caricinus F. Muell.	1	100	1.0	U, N
Solenaceae				
Nicotiana megalosiphon Van Heurk & Müll. Arg.	12 (8)	83	21.5 ± 10.2	F
Nicotiana velutina H.-M. Wheeler	17 (5)	65	12.5 ± 3.8	F
Solanum ellipticum R.Br.	4 (1)	75	3.8 ± 1.3	U
Verbenaceae				
Glandularia aristigera (S. Moore) Tronc.	5 (1)	20	4.0	U, N
Zygophyllaceae				
Zygophyllum tesquorum J.M. Black	1	100	11.0	U

For N samples, numbers in parentheses are those reported in Zalucki *et al.* (1994), which have been incorporated in these data. Host plant status: U = uncertain (<6 samples), G = good, F = fair, P = poor, N = new host record (not sampled by *Zalucki et al.* 1994, or sampled then with negative results).

Table 3 Number of samples, percentage of positive samples, mean numbers per positive sample and putative status of host plants for *H. armigera*

Host plant	*N* samples	% + ive	Mean ± s.e.	Host status
Amaranthaceae				
Ptilotus macrocephalus (R.Br.)Poir	6 (2)	17	0.5	P
Apiaceae				
Eryngium plantagineum F. Muell.	2	50	8.0	U, N
Asteraceae				
Apowollastonia cylindrica Orchard	6 (3)	67	9.8 ± 4.0	G
Brachyscome tetrapterocarpa G.L. Davis	1	100	2.0	P, N
Calotis ancyrocarpa J.M. Black	6 (5)	17	1.4	P
Calotis cuneifolia R.Br.	24 (14)	4	2.0	P
Calotis multicaulis (Turcz.) Druce	49 (28)	6	0.9	P
Leiocarpa brevicompta (F. Muell.) Paul G. Wilson	17 (12)	6	1.7	P
Podolepis jaceioides (Sims) Voss	8 (8)	38	1.2 ± 0.4	F
Pterocaulum sphacelatum (Labill.) F. Muell.)	11	9	1.3	P, N
Pycnosorus chrysanthus (Schltdl) Sond.	26 (13)	12	1.7	P
Rhodanthe floribunda (A. Cunn. ex DC.) Paul G. Wilson	212 (101)	2	1.5 ± 0.5	P
Rhodanthe stricta (Lindl.) Paul G. Wilson	41 (6)	20	0.8 ± 0.1	P
Senecio lautus G. Forst. ex Willd.	32 (12)	3	1.3	P, N
Senecio platylepis DC.	6 (4)	50	2.5 ± 0.2	F
Sonchus oleraceus L.	8 (7)	25	12.2 ± 11.8	G*
Sphaeranthus indicus L.	1	100	3.3	U, N
Verbesina encelioides (Cav.) Benth. & Hook. F. ex A. Gray	23 (2)	9	2.6 ± 1.3	P, N
Xerochrysum bracteatum (Vent.) Tzvelev	8	13	1.3	P
Boraginaceae				
Echium plantagineum L.	28 (13)	7	1.0 ± 0.3	P
Fabaceae				
Aeschynomene indica L.	5	40	19.0 ± 5.0	U, N
Crotalaria dissitiflora Benth.	11	9	1.2	P, N
Cullen cinereum (Lindl.) J.W. Grimes	325 (17)	4	2.2 ± 0.6	P
Medicago polymorpha L.	44 (18)	2	0.3	P
Sesbania brachycarpa F. Muell.	5	80	2.9 ± 0.6	U, N
Swainsona campylantha F. Muell.	4	50	3.7 ± 1.3	U, N
Trigonella suavissima Lindl.	14	7	0.8	P, N
Goodeniaceae				
Velleia glabrata Carolin	66 (46)	8	1.5 ± 0.9	P
Malvaceae				
Malva parviflora L.	3	33	0.5	U, N
Malvastrum americanum (L.) Torr.	41 (4)	5	0.8 ± 0.3	P
Sida ammophila F. Muell. ex J.H. Willis	8 (3)	13	8.0	G*, N
Sida trichopoda F. Muell.	8	25	1.9	P, N
Solenaceae				
Nicotiana megalosiphon Van Heurk & Müll. Arg.	12 (8)	17	1.9 ± 1.1	P

For N samples, numbers in parentheses are those reported in Zalucki *et al.* (1994), which have been incorporated in these data. Host plant status: U = uncertain (<6 samples), G = good, G* = good but rarely utilised, F = fair, P = poor, N = new host record (not sampled by Zalucki *et al.* 1994, or sampled then with negative results).

species came from grassland or mulga habitats in the east of the study area.

Stony downs samples were significantly less likely to be positive for *H. punctigera* than those from sandy deserts, and saltbush sites were significantly less likely to be positive than all other habitats. However, there were no significant differences between sandy deserts, floodplains, mulga and grasslands. There were however large differences in the mean numbers of larvae per 100 sweeps, in the order sandy deserts > floodplains > mulga, grasslands and saltbush > stony downs.

The good host plants varied between habitats, and some hosts which were classed as 'good' in particular habitats were not classed as such in the overall analysis (Figs 5 and 7, Table 2). In sandy deserts, the good hosts were *Polycalymma stuartii*, *Senecio gregorii* and *Rhodanthe charsleyae*, all annual daisies. In the floodplains, they were the annual daisy *Rhodanthe floribunda* and the predominantly annual legume *Cullen cinereum*. In mulga, the good hosts were *C. cinereum* and *R. floribunda* and in grasslands *R. floribunda* and *Apowollastonia cylindrica*. In stony downs, the good hosts were *C. cinereum* and *Senecio magnificus*, and in saltbush the only good host was *C. cinereum*, though it was infrequently utilised (only one positive in eight samples, but with 116 larvae per 100 sweeps recovered). Similarly, the status of particular hosts varied between habitats (Fig. 7). *C. cinereum* emerged as a good host in floodplains, mulga, saltbush and stony downs, but only a fair host in sandy deserts and grasslands. *S. gregorii* was a good host in sandy deserts and mulga, but only a fair one in saltbush and floodplains,

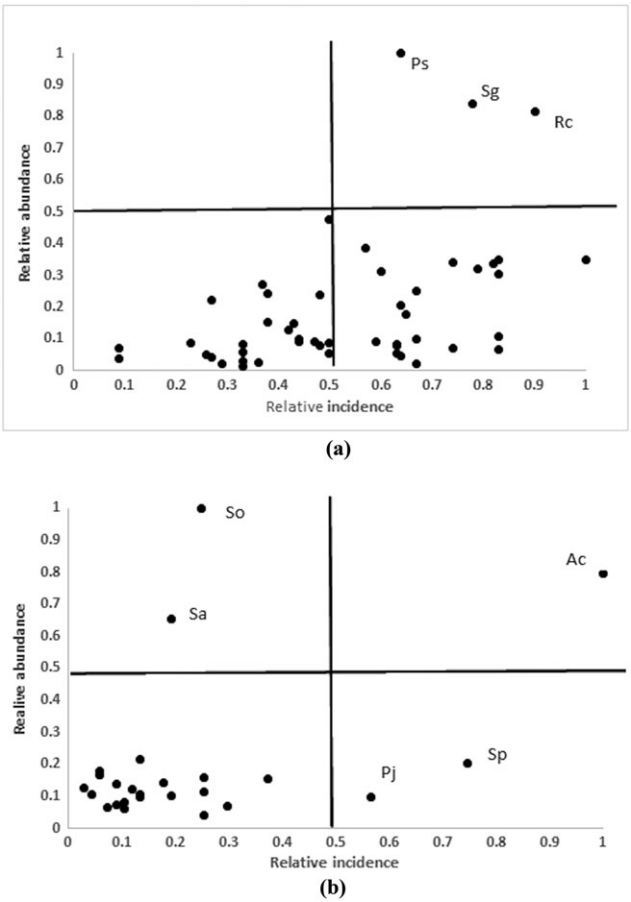

Fig. 5. Status of host plants that were sampled at least six times for *H. punctigera* (a) and *H. armigera* (b), across all habitats. Good hosts are identified for both species, and additionally fair hosts for *H. armigera*: Ps, *Polycalymma stuartii*; Sg, *Senecio gregorii*; Rc, *Rhodanthe charsleyae*; Ac, *Apowollastonia cylindrica*; So, *Sonchus oleraceus*; Sa, *Sida ammophila*; Sp, *Senecio platylepis*; PJ, *Podolepsis jaceioides*.

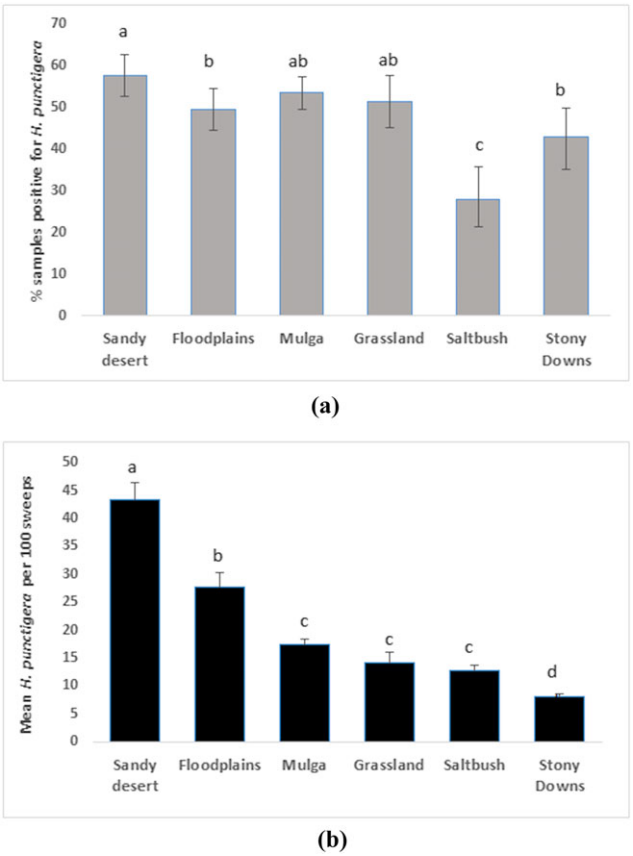

Fig. 6. (a) Percentage of positive samples and (b) mean numbers of *H. punctigera* larvae per 100 sweeps, for all positive samples in six habitats, sandy deserts, floodplains, mulga, grasslands, saltbush and stony downs. Bars for percentages of positive samples are 95% confidence intervals, and bars for mean numbers are standard errors. Columns with different letters are significantly different ($P < 0.05$) by χ^2 tests for percentages and one-way AoV on log transformed data followed by Fishers multiple comparison of means for numbers. [Colour figure can be viewed at wileyonlinelibrary.com]

and was too rare in stony downs and grasslands to enable sufficient samples to be made. Similarly, *P. stuartii* was a good host in the sandy deserts but was rarely seen in other habitats.

DISCUSSION

Constraints of the methodology

This study has added considerably to the host records of *H. punctigera* and *H. armigera*, through sampling new hosts. It has also clarified the host status of some plants by adding to the samples previously reported by Zalucki *et al.* (1994), and it has provided new insights into the key hosts for *H. punctigera* in different habitats of inland Australia. Nevertheless, there are limitations in the methodology which indicate a need for caution in determining host status of these and other polyphagous insects.

Cunningham and Zalucki (2014) review the considerations in determining host status for heliothine moths. Attractiveness to moths, and oviposition by them, does not necessarily indicate that a plant is a host, because *H. armigera* and *H. punctigera* will oviposit on non-host species. Even the presence of small larvae does not confirm host status, because while the early instars of lepidopteran larvae are often characterised by high mortality (Zalucki *et al.* 2002) some larvae may be present for a short time even on non-hosts. Our use of sweep nets minimises these difficulties because they are likely to preferentially catch larger larvae, as very small ones can escape detection when the catch is sorted.

However, sweep nets present other difficulties. They are a relative sampling method, and their efficiency depends on characteristics of the host plant and the behaviour of larvae (Southwood 1978). In particular, they are not suitable for sampling prostrate plants or plants which grow as isolated specimens rather than in clumps. They cannot be used effectively on stiff or spiky plants without risk of damage to the net. Also, they may catch a few larvae on plants that are not hosts. This may occur through contamination of a stand of a non-host with a few host plants that are accidentally swept. We attempted to minimise this

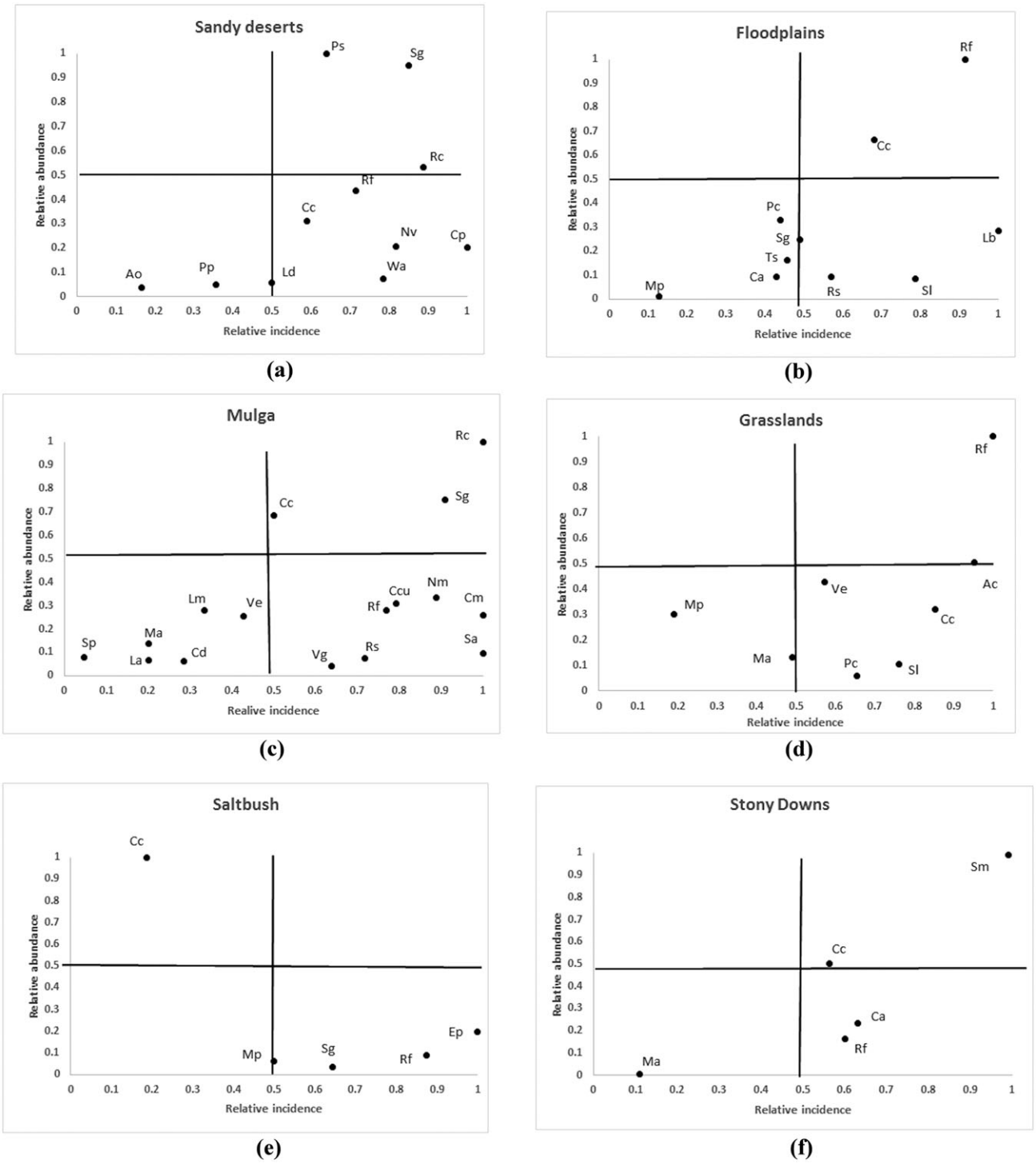

Fig. 7. Host status of plants for *H. punctigera* in (a) sandy deserts, (b) floodplains, (c) mulga, (d) grasslands, (e) saltbush and (f) stony downs. All hosts are identified: Ac, *Apowollastonia cylindrica*; Ca, *Cullen australasicum*; Cc, *Cullen cinereum*; Ccu, *Calotis cuneifolia*; Cd, *Crotalaria dissitiflora*; Cm, *Calotis multicaulis*; Cp, *Cullen pallidum*; Ep, *Echium plantagineum*; Lb, *Leiocarpa brevicompta*; La, *Leucochrysum apiculatum*; Ld, *Lawrencella davenportii*; Lm, *Leucochrysum molle*; Ma, *Malvastrum americanum*; Mp, *Medicago polymorpha*; Nm, *Nicotiana megalosiphon*; Nv, *Nicotiana velutina*; Pc, *Pycnosorus chrysantha*; Pj, *Podolepsis jaceioides*; Pp, *Ptilotus polystachyus*; Ps, *Polycalymma stuartii*; Rc, *Rhodanthe charsleyae*; RF, *Rhodanthe floribunda*; Rs, *Rhodanthe stricta*; Sa, *Sida ammophila*; Sg, *Senecio gregorii*; Sl, *Senecio lautus*; Sm, *Senecio magnificus*; Sp, *Senecio platylepis*; Ts, *Trigonella suavissima*; Ve, *Verbesina encelioides*; Vg, *Velleia glabrata*.

difficulty by selecting relatively pure stands, but in a non-crop environment, it might not always be possible to avoid a few contaminants. Also, larvae of *H. armigera* and *H. punctigera* are quite mobile, especially in the later instars, and will move between plants (Zalucki *et al.* 1986). They may even climb on plants that they are not feeding on, to facilitate behavioural

thermoregulation (Mabbett *et al*. 1980). Thus, the presence of a few larvae in occasional samples does not confirm that a plant is a host. In such cases, the designation as an 'uncertain' host (Tables 2 and 3) means that the uncertainty is whether the plant is a host or not. Similarly, it should not be concluded that all the species where no larvae were found are not hosts. A few negative samples might simply indicate that moths were not present at that location so the plants received no eggs. This is especially the case when closely related species are known to be hosts. Alternatively, it may indicate that all the eggs were deposited on better hosts nearby. However, where repeated sampling yielded no larvae, such as *Brassica tournefortii* (nine negative samples) and *Carrichtera annua* (18 negative samples) in the Brassicaceae, and plants in the Chenopodiaceae generally (collectively 42 negative samples), it is likely that these plants should be regarded as non-hosts.

In other cases (Tables 2 and 3), where there were fewer than six samples but larger mean numbers, the classification of 'uncertain' means the uncertainty centres not on whether the plant is a host, but whether it should be classed as good, fair or poor. In such cases, data for closely related species provide some guidance in assessing host status. For example, there were several daisies in the genus *Rhodanthe* for which insufficient samples were available, simply because stands of these species suitable for sweep netting were uncommon. Since all had at least 4.5 *H. punctigera* larvae per 100 sweeps, and other species in the genus consistently had larger numbers (Table 2), it is likely that these are hosts, and possibly fair or even good ones. However, for the two species of grasses, *Dactyloctenium radulans* and *Amphipogon caricinus*, there was only one positive sample each, and numbers were low (2.9 and 1.0 per 100 sweeps, respectively). As grasses are not generally hosts for *H. punctigera* (Zalucki *et al*. 1986), it is likely that these are false positive results, due to contamination of the sample with genuine hosts or to larval mobility.

The roles of habitats for inland *Helicoverpa punctigera* populations

The most productive habitat for *H. punctigera*, given good conditions for host growth, is clearly the sandy deserts. These had the highest proportion of positive samples and mean numbers of larvae per sample (Fig. 6), and given good rainfall they support extensive areas of good hosts, *Polycalymma stuartii*, *Senecio gregorii* and (to a lesser extent) *Rhodanthe charsleyae*. These annual daisies appear to have seed dormancy mechanisms which limit their germination to cooler months, as is the case for many inland daisies (Hoyle *et al*. 2008). Their abundance therefore depends on the amount of autumn and winter rainfall in central Australia, which is highly variable from year to year (Morton *et al*. 2011). In sandy soils, small falls of rain result in water being quickly but briefly available to plants, favouring those with short growth cycles. Spring and summer rainfall in sandy deserts promotes the growth of grasses and perennial dicots which are generally poor hosts. There are however two annual legumes, *Cullen cinereum* (in clay pans between sand dunes) and *C. pallidum* (on dunes) which are good hosts that respond to summer rain and may allow the persistence of *H. punctigera* through summer. Given the large areas of sandy deserts and the frequent, though irregular, abundance of good hosts, it is likely that in some years this habitat provides many potential emigrants that may infest cropping areas to the east and south, following their long distance movement on westerly or northerly winds in spring (Drake 1994; Gregg *et al*. 1995). While these regions are far from cropping areas (at least 1000 km) and it is probable that some migrations do not reach crops, it is likely that many do (Gregg 1993, Gregg *et al*. 1995). Part of the reason why Baker *et al*. (2011) failed to find correlations between spring immigration in cropping areas and winter rainfall in certain areas of inland Australia may be that they did not include rainfall data from sandy deserts, because these areas are almost uninhabited and have very few meteorological sites.

The floodplains occupy much smaller areas than the other habitats, but they had the second-highest mean numbers of larvae per 100 sweeps (Fig. 6). By far, the most common good host in the central floodplains which drain to the Lake Eyre basin is *Cullen cinereum*, though other legumes and daisies (notably *Rhodanthe floribunda*) are also present. In the eastern floodplains of the Murray–Darling, the most abundant hosts are *Medicago* spp. and daisies such as *Leiocarpa brevicompta*. The floodplains have alluvial soils with high clay contents (Wilson *et al*. 1990), which means that small falls of rain do not become available to plants, and the main stimulus for host germination is inundation from floods resulting from irregular heavy rainfall hundreds of km to the north and east. This means that the floodplains are often devoid of vegetation, or support only dry grasses, but when they are green, they can support hosts even when no local rain has fallen. They can therefore sometimes serve as refuges, where *H. punctigera* populations can persist and later colonise other habitats (Gregg *et al*. 2016).

The mulga habitat is distributed in the east and northwest of the region, though there are patches elsewhere. The reference host here, for both relative abundance and relative incidence, was *Rhodanthe charsleyae*, but it occurs only in the western mulga. In the east, other daisies such as *R. floribunda* and *Calotis* spp. were more common. These supported lower densities of larvae, but because of their abundance in favourable seasons, they probably contributed more to the mulga populations than hosts such as *Cullen cinereum*, which was restricted to creek lines. While the daisies were mainly found following autumn or winter rainfall, the eastern mulga also supported patches of hosts in other families, especially Solanaceae, Goodeniaceae and Geraniaceae. The special significance of the eastern mulga region is that it is the closest habitat to the cropping areas of Queensland and New South Wales, and might serve as a bridge between these areas and the more productive sandy deserts and floodplains. It might support an intervening generation in late winter, founded by immigrants from the west, which could provide moths in spring to infest cropping areas.

The grasslands supported only limited numbers of good hosts. *Cullen cinereum* was present in creek lines and small low lying areas, along with daisies such as *Rhodanthe floribunda* and *Apowollastonia cylindrica*. However, the bulk of the habitat was occupied by grasses which, even when dry, appeared to

restrict the growth of host plants to isolated plants or small patches. It is unlikely that grasslands contributed greatly to potential migrations from the inland.

Saltbush habitats had a significantly lower proportion of positive samples than all the other habitats (Fig. 5). One factor contributing to this is probably that the saltbush plains are the most southerly habitat, and during winter when many of the field trips were conducted they are prone to frosts which can kill eggs and larvae (Zalucki *et al.* 1986). Another factor is that many of the samples were done on chenopods, especially *Atriplex* and *Maireana* spp. which dominate the habitat, and no larvae were ever found on them. The most abundant hosts were *Medicago* spp. but there were also patches of daisies such as *R. floribunda*. It is possible that these hosts may serve the same bridging function as postulated for the mulga in the east, but for a different cropping area: the southern canola and grain legume areas of Victoria and South Australia.

The stony downs are probably the least productive habitat for *H. punctigera*. Hosts were very patchy and largely restricted to creek lines and, while there were more positive samples than in the saltbush plains, the mean numbers per sample were the lowest of any habitat. In terms of island biogeography (MacArthur & Wilson 1967), the stony downs may represent the 'ocean' between islands of more favourable habitat and may play a key role in the evolution of migratory strategies for *H. punctigera* and other insects (Drake *et al.* 1995). One caveat to this is that there are potential hosts in the stony downs that were not sampled: succulents in the families Aizoaceae and Portulaceae. Larvae have been found on some species in these families (Zalucki *et al.* 1986), but not those common in the stony downs. While larvae were occasionally seen crawling on these plants in our work, they were not seen feeding and the plants were too prostrate for sweep netting. There is a need for laboratory studies to determine whether these plants are oviposited on, and whether larvae survive on them.

In only one habitat, saltbush, was there one species, *Cullen cinereum*, in the top left quadrant of the matrix for *H. punctigera* (good but rarely utilised hosts). For all the others individually and for all habitats combined, there were none (Figs 5a and 7). This suggests that this species has an unusual ability to locate host plants over large distances. We sometimes observed small patches of hosts in areas that had received isolated rainfall but were surrounded by hundreds of km of habitat that had remained dry for many months, and supported no hosts. Larvae were often found on these hosts. *H. punctigera* apparently lack dormancy or diapause which would allow them to survive such extended dry periods (Zalucki *et al.* 1986). Though they possess over wintering and over summering pupal diapause mechanisms (Cullen & Browning 1978), these appear to be relatively weak, especially in our study area, (Le Mottee 2015) and unlikely to allow survival over such extended periods, particularly during the warmer months. It is thus likely there were no locally emerging moths to colonise these areas, and therefore, these isolated hosts had been found by ovipositing moths coming from great distances.

In the case of *H. armigera*, there were two hosts in the good but rarely used category. They were species which occur throughout the study area, but yielded larvae only in the eastern areas. Their categorisation probably reflects their wide distribution, in conjunction with the rarity of *H. armigera* in most of the study area, rather than their intrinsic suitability as hosts. One of these plants, *Sonchus oleraceus*, has been proposed as a primary host for *H. armigera* on the basis of laboratory studies of oviposition preferences and larval survival (Gu & Walter 1999).

Rarity of *H. armigera* in the inland

There is an apparent gradient in abundance of *H. armigera* from eastern and northern Australia, where they frequently cause problems on crops, to the south and east where, despite occasional specimens in pheromone traps (Fitt *et al.* 1995), they are rare and do not usually cause serious damage to crops (Zalucki *et al.* 1986). In our study, *H. armigera* were mostly found in the north-east of the study area (Fig. 4), and the species which emerged as good or fair hosts were generally restricted to this region. Species common in the central and western areas had few if any *H. armigera*. For example, a good host for *H. punctigera* in the sandy deserts, *Polycalymma stuartii*, was sampled 91 times (Table 2), and of over 3000 larvae reared from this host, not one proved to be *H. armigera*.

This suggests that *H. armigera* is not well adapted to the environment of far inland Australia. This could in principle be due to poor adaptation to the hosts. Given the extreme polyphagy of *H. armigera* and the similarity at family level of its host range to that of *H. punctigera* (Cunningham & Zalucki 2014) this seems unlikely, but there is a need for laboratory studies on oviposition preferences (relative to crops) and survival of larvae on inland host plants. It is more likely that some other life history traits of *H. armigera* limit its adaptation to the inland environment. Differences in migration strategy between *H. armigera* and *H. punctigera* may play a role. While *H. armigera* is clearly capable of long-distance migration (Gregg 1995), it is thought to be less migratory than *H. punctigera*, and more of a facultative migrant (Farrow & Daly 1987). Perhaps this strategy is inadequate in the extremely variable environment of central Australia, particularly in regard to locating isolated host patches. In any case, the relative lack of *H. armigera* in our study suggests that migration from the inland is much less important for this species than it is for *H. punctigera*, and pest management strategies should focus more on manipulation of populations within the cropping regions than on dealing with immigrants.

Host plant status and applications of the incidence/abundance matrix

Zalucki *et al.* (1994) suggested that the incidence/abundance matrix could be used to identify 'key' or 'primary' hosts of polyphagous species, which would be located in the upper right quadrant of the matrix. There are a number of difficulties with this, although it is clear that the approach can provide valuable insights. One difficulty is that the terms 'key' and 'primary' are not well defined. Walter and Benfield (1994) describe a primary host as one which contributes substantially and regularly to populations in a given region. They identify *Leiocarpa* (=*Ixiolaena*) *brevicompta* as such a host for *H. punctigera* in cropping areas of

southern Queensland and northern New South Wales, on the eastern margin of our study area. Elsewhere (Gu & Walter 1999; Walter 2005), it is suggested that a primary host is one which is favoured for oviposition and allows good survival of larvae, characteristics which derive from a close co-evolutionary relationship with the insect. Our study indicates that the two interpretations are not synonymous. We propose that 'primary host' should be used to indicate evolutionary relationships and 'key host' should be reserved for hosts that strongly affect population dynamics, in a similar sense to the way 'key pest' is used in integrated pest management to identify a pest which sets the parameters for management tactics (e.g. Fitt 2000).

Our study suggests that the matrix is of little value for determining evolutionary relationships, and therefore primary hosts. Phylogenetic evidence indicates that generalists do not often evolve from specialists; the reverse is more common, though more recent models suggest that periods of selection towards specialisation might be interspersed with selection towards polyphagy (Jermy 1984; Janz *et al*. 2006). Other factors including learned behaviour and physiological state of the insects (Cunningham & Zalucki 2014) also complicate the inference of co-evolutionary relationships from incidence and abundance data.

The reliance on outliers to set the maximum for abundance can result in a few samples having disproportionate influence. For example, the identification of *Cullen cinereum* as a good, if infrequently used, host in saltbush habitats (Fig. 5) depended on one positive sample, out of eight, which yielded many larvae. Had this sample not been made, *C. cinereum* would have been considered a poor host in this habitat and the positions of other plants in the matrix would have been very different. Other factors which may affect host suitability include nearby plants and their phenological state. Gregg *et al*. (2016) found that when *C. cinereum* or *C. pallidum* was found near daisies in the western floodplains, the legume had more larvae if both the daisy and the legume were flowering, but this was reversed if only the daisy was flowering. Phenological asynchrony can occur between floodplains and adjacent habitats such as sandy deserts and stony downs because germination in the floodplains can be initiated by rain falling only in distant areas. It is for such reasons that the hosts in the top right quadrant of the matrix are different for different habitats, and that *L. brevicompta*, proposed as a primary host by Walter and Benfield (1994), did not emerge as such in any of our habitats. Thus, we avoid the use of 'primary' or 'key' hosts in relation to the matrix and describe plants in the top half as 'good' hosts.

The matrix may be more useful for identifying key hosts, which strongly influence population dynamics. Even for this purpose, though, it must be considered along with other evidence. The distribution and abundance of plants must be considered along with their suitability in any assessment of their role in broad scale population dynamics. Key hosts do not only have to be 'good' (or at least 'fair') – they also have to be widespread and abundant, or available at times or places where there are few other hosts. For example, *Rhodanthe charsleyae* is a good host, but its distribution is restricted to the western third of the study area (Atlas of Living Australia 2017, https://www.ala.org.au/). It is probably less important quantitatively and in regard to migration to cropping areas (from which it is very distant) than *Rhodanthe floribunda*, which is widely distributed and common in several habitats, including those closer to cropping areas. Similarly, in the mulga *Senecio gregorii* and *Cullen cinereum* are good hosts, but they are rare and probably contribute much less to the population than species such as *Velleia glabrata*, *Rhodanthe stricta* and *Calotis multicaulis*. Those species had relatively low mean numbers of larvae per 100 sweeps, probably because they are small spindly plants which do not form a dense ground cover. However, they are widespread in the eastern mulga regions and abundant following good autumn or winter rain.

When all these factors are taken into consideration, we believe that a short list of the key hosts would include *Polycalymma stuartii*, *Senecio gregorii* and *Rhodanthe floribunda* in the sandy deserts, *Cullen cinereum* in the floodplains, *Rhodanthe floribunda*, *Calotis multicaulis* and *Velleia glabrata* in the mulga and *Rhodanthe floribunda* and *Medicago* spp. in the grasslands and saltbush.

CONCLUSIONS

Helicoverpa punctigera is widely distributed in inland Australia and has an extensive and diverse range of native non-crop host plants. Some hosts are abundant and widespread, others are less common and localised. This study has extended the list of host records for *H. punctigera* and clarified the status of some previously known hosts. We identified six main habitats for *H. punctigera* in the inland and showed that the key hosts were different in each of them. The most productive habitats were sandy deserts, floodplains and mulga, and each plays a particular role in broad scale population dynamics.

The diversity and suitability of hosts for *H. punctigera*, along with its known capacity for long distance migration, suggests that pest management in cropping areas should be focused on preparing for, detecting and responding to immigration from non-cropping areas. Preparation can include choosing less susceptible crops or varieties, and manipulation of planting dates to avoid the coincidence of susceptible growth stages and potential immigration. Detection includes forecasting systems based on ecological insights such as those described in this paper, early warning devices such as pheromone and light traps, and frequent crop monitoring. Responses are likely to emphasise pesticides, and this species (in contrast to *H. armigera*) has little history of resistance to insecticides. However, choosing the least disruptive ones, such as biopesticides, will foster integrated pest management and avoid outbreaks of secondary pests.

In contrast, *H. armigera* was rare and found mostly in the eastern inland. There is a need for further studies on oviposition preferences and larval survival of *H. armigera* on native hosts to determine the reasons for this rarity. Management of this species should focus on manipulation of populations within cropping areas, and responses such as habitat modification to enhance natural enemy activity and cultural measures targeting overwintering pupae will be more important contributors to integrated pest management.

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