SHORT COMMUNICATION

Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand

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Abstract: The idea that naturalised invading plants have fewer phytophagous insects associated with them in their new environment relative to their native range is often assumed, but quantitative data are few and mostly refer to pests on crop species. In this study, the incidence of seed-eating insect larvae in flowerheads of naturalised Asteraceae in New Zealand is compared with that in Britain where the species are native. Similar surveys were carried out in both countries by sampling 200 flowerheads of three populations of the same thirteen species. In the New Zealand populations only one seed-eating insect larva was found in 7800 flowerheads (0.013% infected flowerheads, all species combined) in contrast with the British populations which had 487 (6.24%) flowerheads infested. Possible reasons for the low colonization level of the introduced Asteraceae by native insects in New Zealand are 1) the relatively recent introduction of the plants (100-200 years), 2) their phylogenetic distance from the native flora, and 3) the specialised nature of the bud-infesting habit of the insects.

Keywords: Asteraceae, insect colonization, introduced plants, New Zealand, seed predation, weed invasion.

Introduction

Invading plant species may often have the advantage of escaping the phytophagous insects which normally feed on them in their places of origin (Moran, 1980; Strong *et al.,* 1984; Crawley, 1987; Drake *et al*., 1989). However, in their new territories they may face exploitation by native insects. Studies on a range of cases around the world (Strong *et al*., 1984) show that some introduced plants can be colonised relatively quickly, usually by less specialised (polyphagous), chewing or sucking insects. In other cases, even long-established aliens appear to have acquired few or no herbivores (Strong, 1979; Moran, 1980). Factors which are thought to determine the likelihood of exotic plants being colonised by native insects in new habitats are (a) the size of the area invaded or planted, and (b) the taxonomic closeness of the introduced plant to species within the native flora (Strong *et al*., 1984; Mack, 1996).

The naturalised flora of New Zealand (Webb *et al*., 1988) offers many opportunities for investigating both the degree to which alien species are free of their original burden of herbivorous insects, and the level of acquisition of new 'natural enemies' from the native insect fauna. Over the last two centuries, the New Zealand flora has seen a spectacular invasion of exotic species, especially by temperate grassland and open habitat species from Europe and North America. Among naturalised flora of New Zealand, the Asteraceae are well represented by over 220 species (Webb *et al*., 1988). In many Asteraceae, the flowerheads (capitula) during seed maturation are often exploited by the larvae of seed-eating insects (Fenner, 1999). These seed-predators are readily detected by dissecting mature flowerheads, and this provides a convenient means of making comparisons between the levels of populations of the same species in their native and non-native territories. Comparative quantitative data showing that populations of successful plant invaders are attacked by fewer herbivores than conspecific populations in their native regions are rare. This study consists of a comparison between the incidence of pre-dispersal seed predators in populations of introduced Asteraceae in New Zealand and that of home range populations in Britain.

Materials and methods

Three populations each of thirteen species of common grassland Asteraceae were sampled both in South Island, New Zealand (in January and February 1998) and in southern Britain (in July and August 1997). The species chosen are native to Britain, have a wide distribution in northern temperate climates, and have been accidentally introduced to New Zealand, largely as pasture and open-habitat weeds. Most have been well established as naturalised aliens since the early days of European colonisation (*ca.*150-200 years). In each population, 200 flowerheads were collected in mid-season for the species. Only fully opened (but unwithered) flowerheads showing no external sign of damage were chosen. At each site, flowerheads were gathered at random from a large number of separate individual plants. Each flowerhead was examined by dissecting it vertically through the receptacle and noting the presence or absence of seed-eating insects. The latter consisted largely of sedentary, flowerbud-infesting fly larvae (Diptera). No formal identification of the larvae was made because the focus of the study was the frequency with which flowerheads suffered infestation.

Results

Table 1 shows the species sampled, the general locations (see Appendix for details) of the populations, and the percentage of flowerheads containing seed-eating larvae. The British populations show a much higher level of infestation. Ten of the 13 species sampled from

Table 1. Percent infestation of capitula in populations of 13 species of herbaceous Asteraceae at three locations in New Zealand and Britain. *N*=200 at each location.

	New Zealand				United Kingdom			
	Location 1	Location 2	Location 3	Mean	Location 1	Location 2	Location 3	Mean
Achillea millefolium L.	Burwood 0%	Dunedin 0%	Lincoln 0%	0%	Totton 0%	Mainsbridge 0%	Southampton 0%	0%
Bellis perennis L.	Invercargill 0%	Dunedin 0%	Te Anau 0%	0%	Highfield 0%	Chilworth 5.0%	Southampton 1.5%	2.17%
Cirsium arvense (L.) Scop.	Te Anau 0%	Dunedin 0%	Lincoln 0%	0%	Totton 1.5%	Chilworth 1.0%	Bassett Green 0%	0.83%
Cirsium vulgare (Savi) Ten.	Invercargill 0%	Portobello 0%	Te Anau 0%	0%	Totton 2.0%	Mainsbridge 28.0%	Ashurst 4.0%	11.3%
Crepis capillaris (L.) Wallr.	Burwood 0%	Dunedin 0%	Lincoln 0%	0%	Chilworth 6.0%	Highfield 0%	Totton 1.5%	2.5%
Hieracium pilosella L.	Burwood 0%	Waterloo 0%	Oreti Valley 0%	0%	Lordshill 0%	Southampton 0.5%	Bassett 0%	0.17%
Hypochaeris radicata L.	Invercargill 0%	Dunedin 0%	Burwood 0%	0%	Highfield 0%	Totton 3.0%	Denny 2.5%	1.83%
Lapsana communis L.	Dunedin 0%	Springfiled 0%	Dunedin 0%	0%	Totton 0%	Southampton 0%	Highfield 0%	0%
Leucanthemum vulgare Lam.	Dunedin 0%	Burwood 0%	Springfield 0%	0%	Winchester 35.5%	Farley Mount 30.5%	Bassett Green 12.0%	26.0%
Senecio jacobaea L.	Westport 0%	Mossburn 0%	Oamaru 0.%	0%	Totton 0%	Southampton 1.5%	Mainsbridge 2.5%	1.33%
Senecio vulgaris L.	Dunedin 0%	Burwood 0%	Oamaru 0.5%	0.17%	Highfield 0%	Totton 0%	Portswood 0%	0%
Taraxacum officinale Weber	Invercargill 0%	Dunedin 0%	Wendonside 0%	0%	Highfield 0%	Mainsbridge 3.0%	Southampton 3.0%	2.0%
Tripleurospermum inodorum Schultz Bip.	Mossburn 0%	Brighton 0%	Lincoln 0%	0%	Totton 23.5%	Mainsbridge 48.0%	Beaulieu 27.5%	33.0%
Summary								
Percentage of flowerheads infested (n = 7800)				0.012				6.24
Number of species with infested flowerhead (n = 13)				1				10

Britain show some infestation, compared with only one in New Zealand. British levels of infestation range from zero (in three species) to 48% in one of the populations of *Tripleurospermum inodorum* Schultz Bip with an overall average of 6.24% of flowerheads infested. In the New Zealand samples, only one flowerhead (0.12% of those sampled) was found to be infested - by a larva of the fruitfly *Tephritis fascigera* Malloch. (Diptera: Tephritidae) in groundsel (*Senecio vulgaris* L.).

Discussion

Although the scale of this survey is small, the data presented here do provide some evidence that populations of introduced species of herbaceous Asteraceae in New Zealand carry a much lighter burden of seed predators than conspecific populations in their native environments. The mode of arrival of these invading plant species (probably as contaminants in imported seed) may not have provided an opportunity for the flower-bud infesting insects to accompany them to their new location. A more widespread and detailed survey over a longer period would undoubtedly reveal more cases of infestation in New Zealand, but the overall contrast between the New Zealand and British populations would probably remain. Whether or not the lack of seed predation in the species tested has contributed to their invasion success is unknown. Seed loss would only affect regeneration if recruitment was seed-limited (Anderson, 1989; Williamson and Fitter, 1996).

The native New Zealand Asteraceae have their own pre-dispersal seed predators, the most conspicuous of which are the Trypetid flies (Diptera) which infest *Celmisia*, *Raoulia* and native *Senecio* species (Molloy, 1975). Burrows (1961) records flowerheads of *Celmisia* species infested with a range of insects, including Lepidoptera, Hemiptera, Diptera and Coleoptera. Some of these native insects may occasionally infest the introduced Asteraceae. The one larva found on the introduced *S. vulgaris* here is native to New Zealand, and Syrett and Smith (1998) reported many native phytophagous insects associated with introduced *Hieracium* species, though none of the specialised European fauna was found.

However, the general widespread absence of seed-eating larvae in introduced species in New Zealand (compared with their abundance on native Asteraceae species) suggests that the native seed predators have not been able to transfer readily to the alien plants. A similar failure of native Californian insects to colonise the invasive thistle *Carduus pycnocephalus* L. has also been reported (Goeden, 1974).

The failutre of native insects to colonize the invading plant species may be partly due to the comparatively recent arrival of these aliens in New Zealand. The time since introduction (150-200 years) may not be long enough to allow for adaptation by the local insect fauna to the novel host, though for many crop species this period is sufficient for some colonization (Strong *et al*., 1984). It is also possible that the introduced species of Asteraceae investigated here are not sufficiently closely related to any native species to allow such transfers to take place readily. Colonization is more likely if the phylogenetic distance between the new-comers and the native flora is not too great (Mack, 1996). Amongst the plants included in this study, the only genera which are represented in the native New Zealand flora are *Senecio* (40 species) and *Taraxacum* (one species) (Allan, 1961). It is therefore interesting to note that the only instance we found of an alien plant being exploited by a native insect in this survey involved a *Senecio,* and that the Dipteran (*Tephritis fascigera* Malloch) which had made the transition is normally associated with native genera formerly included within *Senecio* (e.g. *Brachyglottis kirkii* (Kirk) C. Webb). The larva are also associated with native Asteraceous shrubs (e.g. *Ozothamnus vauvilliersii* Homb. et Jacq.), and the invasive introduced herb *Ageratina adenophora* (Sprengel) R. King et H. Robinson.

Another reason for the low colonisation of the alien Asteraceae may be that it is more difficult for highly host-specific, bud-infesting, seed-eating insects to adapt to a new host plant than it would be for a more generalised, folivorous species. The first insects to attack newly introduced crops tend to be chewing and sucking external feeders rather than leaf miniers and gall formers (Strong *et al*., 1984). Most phytophagous insects have a very restricted range of host plants (Andow and Imura, 1994), possibly as a result of a chemical "arms race" between plant and insect (Cates, 1980), or reduced predation on the insect (Bernays and Graham, 1988). Phytophagous insect recruitment curves on alien plants reach equilibrium at an average estimated lives of 100 generations for generalists and 500-10,000 generations for specialists (Southwood, 1984; Strong *et al*., 1984). The seed-eating insects in this study occupy a rather narrow, specialised niche, which may make them less flexible in adapting to new situations.

A wider survey, encompassing more species of plant, and a wider variety of associated insects (especially less specialised externally feeding species), may reveal a greater level of exploitation of alien plants by native New Zealand insects. It would be of particular interest to test the ideas of Strong *et al*. (1984) by investigating how time since first introduction and area of current distribution affect the levels of colonization.

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Appendix. Sampling dates and latitude and longitude references for populations of all species used in the study.

	Location 1	Location 2	Location 3	Location 1	Location 2	Location 3
Achillea millefolium L.	Burwood 22/1/98 lat. 45E 33' 40" long. 168E 01' 33"	Dunedin 27/1/98 lat. 45E 51' 57" long. 170E 30' 53"	Lincoln 30/1/98 lat. 43E 38' 32" long. 172E 28' 27"	Totton 3/7/97 lat. -1E 29' 16" long. 50E 55' 9"	Mainsbridge 17/7/97 lat. -1E 21' 50" long. 50E 56' 9"	Southampton 10/7/97 lat. -1E 24' 34" long. 50E 55' 57"
Bellis perennis L.	Invercargill 3/1/98 lat. 46E 22' 48" long. 168E 21' 14"	Dunedin 6/1/98 lat. 45E 51' 48" long. 170E 30' 44"	Te Anau 22/1/98 lat. 45E 25' 17" long. 167E 42' 50"	Highfield 1/7/97 lat. -1E 24' 34" long. 50E 56' 6"	Chilworth 26/6/97 lat. -1E 18' 33" long. 50E 57' 48"	Southampton 2/7/97 lat. -1E 23' 43" long. 50E 55' 50"
Cirsium arvense (L.) Scop.	Te Anau 22/1/98 lat. 45E 25' 17" long. 167E 42' 50"	Dunedin 27/1/98 lat. 45E 51' 18" long. 170E 30' 27"	Lincoln 30/1/98 lat. 43E 38' 32" long. 172E 28' 27"	Totton 4/7/97 lat. -1E 29' 6" long. 50E 55' 13"	Chilworth 9/7/97 lat. -1E 18' 39" long. 50E 57' 48"	Bassett Green 9/7/97 SU 424164 lat. -1E 23' 47" long. 50E 56' 42"
Cirsium vulgare (Savi) Ten.	Invercargill 3/1/98 lat. 46E 22' 48" long. 168E 21" 14"	Portobello 25/1/98 lat. 45E 50' 30" long. 170E 39' 08"	Te Anau 22/1/98 lat. 45E 24' 55" long. 167E 44' 29"	Totton 4/7/97 lat. -1E 29' 16" long. 50E 55' 6"	Mainsbridge 18/7/97 lat. -1E 21' 45" long. 50E 56' 9"	Ashurst 17/7/97 lat. -1E30' 34" long. 50E 53' 33"
Crepis capillaris (L.) Wallr.	Burwood 22/1/98 lat. 45E 33' 40" long. 168E 01' 33"	Dunedin 3/2/98 lat. 45E 51' 48" long. 170E 30' 44"	Lincoln 30/1/98 lat. 43E 38' 32" long. 172E 28' 27"	Chilworth 24/6/97 lat. -1E18' 33" long. 50E 57' 51'	Highfield 1/7/97 lat. -1E 24' 34" long. 50E 56' 16"	Totton 3/7/97 lat. -1E 29' 11" long. 50E 55' 13"
Hieracium pilosella L.	Burwood 22/1/98 lat. 45E 33' 40" long. 168E 01' 33"	Waterloo 4/2/98 lat. 45E 41' 59" long. 167E 59' 50"	Oreti Valley 18/2/98 lat. 45E 25' 18" long. 168E 08' 11"	Lordshill 27/6/98 lat. -1E 25' 40" long. 50E 56' 7"	Southampton 2/7/98 lat. -1E 24' 50" long. 50E 55' 15"	Bassett 20/6/98 lat. -1E 24' 13" long. 50E 56' 10"
Hypochaeris radicata L.	Invercargill 2/1/98 lat. 46E 22' 48" long. 168E 21' 14"	Dunedin 6/1/98 lat. 45E 51' 48" long. 170E 30' 44"	Burwood 22/1/98 lat. 45E 33' 40" long. 168E 01' 33"	Highfield 7/7/97 lat. -1E 24' 34" long. 50E 56' 13"	Totton 3/7/97 lat. -1E 29' 11" long. 50E 55' 9"	Denny 3/7/97 lat. -1E 31' 31" long. 50E 51' 33"
Lapsana communis L.	Dunedin 28/1/98 lat. 45E 50' 19" long. 170E 29' 52"	Springfield 4/2/98 lat. 43E 20' 16" long. 171E 55' 45"	Dunedin 16/2/98 lat. 45E 51' 52" long. 170E 31' 21"	Totton 31/7/97 lat. -1E 29' 11" long. 50E 55' 16"	Southampton 23/7/97 lat. -1E 24' 29" long. 50E 55' 47"	Highfield 2/7/97 lat. -1E 24' 28" long. 50E 56' 13"
Leucanthemum vulgare Lam.	Dunedin 6/1/98 lat. 45E 49' 17" lang. 170E 32' 14"	Burwood 22/1/98 lat. 45E 33' 40" long. 168E 01' 33"	Springfield 4/2/98 lat. 43E 20' 16" long. 171E 55' 45"	Winchester 13/6/97 lat. -1E 18' 19" long. 51E 2' 52"	Farley Mount 13/6/97 lat. -1E 24' 2" long. 51E 3' 46"	Bassett Green 14/6/97 lat. -1E 23' 42" long. 50E 56' 51"
Senecio jacobaea L.	Westport 11/2/98 lat. 41E 45' 16" long. 171E 37' 23"	Mossburn 23/1/98 lat. 45E 39' 37" long. 168E 13' 09"	Oamaru 9/2/98 lat. 45E 05' 59" long. 170E 57' 54"	Totton 3/7/97 lat. -1E 28' 35" long. 50E 55' 9"	Southampton 12/7/97 lat. -1E 24' 34" long. 50E 55' 40"	Mainsbridge 18/7/97 Lat. -1E 21' 50" long. 50E 56' 12"
Senecio vulgaris L.	Dunedin 3/2/98 lat. 45E 51' 57" long. 170E 30' 48"	Burwood 22/1/98 lat. 45E 33' 40" long. 168E 01' 33"	Oamaru 9/2/98 lat. 45E 05' 59" long. 170E 57' 54"	Highfield 20/8/97 lat. -1E 23' 43" long. 50E 55' 56"	Totton 3/7/97 lat. -1E 29' 11" long. 50E 55' 6"	Portswood 23/8/97 lat. -1E 23' 17" long. 50E 55' 50"
Taraxacum officinale Weber	Invercargill 2/1/98 lat. 46E 22' 48" long. 168E 21' 14"	Dunedin 15/1/98 lat. 45E 51' 48" long. 170E 30' 44"	Wendonside 23/1/98 lat. 45E 45' 29" long. 168E 40' 19"	Highfield 15/9/97 lat. -1E 24' 28" long. 50E 56' 13"	Mainsbridge 18/9/97 lat. -1E 21' 44" long. 50E 56' 12"	Southampton 21/9/97 lat. -1E 24' 13" long. 50E 55' 40"
Tripleurospermum inodorum Schultz Bip.	Mossburn 23/1/98 lat. 46E 22' 48" long. 168E 21' 14"	Brighton 1/2//98 lat. 45E 57' 00" long. 170E 19' 45"	Lincoln 30/1/98 lat. 43E 38' 32" long. 172E 28' 27"	Totton 4/7/97 lat. -1E 29' 11" long. 50E 55' 6"	Mainsbridge 18/7/97 lat. -1E 21' 45" long. 50E 56' 5"	Beaulieu 18/7/97 lat. -1E 27' 12" long. 50E 49' 6"