

SHORT COMMUNICATION

Novel host associations and habitats for *Senecio*-specialist herbivorous insects in Auckland

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Abstract: We studied the genus- and species-specialist monophagous herbivorous insects of *Senecio* (Asteraceae) in Auckland, New Zealand. With the exception of the widespread *S. hispidulus*, the eight native *Senecio* species in mainland Auckland (two endemic) are typically uncommon and restricted to less modified conservation land. However, 11 naturalised *Senecio* have established and are often widespread in urban and rural habitats. Three endemic *Senecio*-specialist herbivores – *Nyctemera annulata*, *Patagoniodes farnaria*, and *Tephritis fascigera* – formed novel host associations with naturalised *Senecio* species and spread into modified landscapes. Host associations for these species were not related to whether *Senecio* species are naturalised or native. However, the abundances of *Patagoniodes farnaria* and *Tephritis fascigera* were significantly higher in wildland habitats than rural or urban habitats, and wildland *Senecio* were on average 1.4 times more likely to experience >5% folivory than urban conspecifics.

Keywords: biological control; Asteraceae; invasion; monophagy; naturalisation; *Stigmella ogygia*; weed

Introduction

Many native New Zealand insects may be host- and habitat-specialised to the extent that they fail to utilise the rural and urban habitats that now dominate New Zealand. In his landmark study of beetles in suburban Auckland, Kuschel (1990) found a strong disjunction between beetle assemblages in native forest habitats versus in neighbouring suburban habitats. Only 9% of the 753 non-littoral native beetle species Kuschel collected were found outside of native forest in suburban Auckland. Subsequent studies have found a similar dependence of native insects on native forest habitats (Harris & Burns 2000; Derraik et al. 2005; cf. Harris et al. 2004).

Such habitat specialisation can prevent monophagous insect herbivores from occurring on their host plants when these are cultivated in urban and rural landscapes. Kuschel (1990) failed to find 20 monophagous herbivorous beetle species on their host plants in Auckland suburban gardens, despite their commonness in local native forest and their native host plants commonly planted in local gardens.

Urban and rural habitats in New Zealand tend to be dominated not just by naturalised insects but also naturalised plants (e.g. Esler 1988, 2004; Webb et al. 1988).

The enemy release hypothesis (e.g. Keane & Crawley 2002; Clay 2003) claims that many naturalised plants become invasive and dominate over native species because they have escaped from their natural enemies in their native ranges. Specialist herbivore species of broom, *Cytisus scoparius*, are both more diverse and more abundant in the native (France and England) than the naturalised range (Australia and New Zealand; Memmott et al. 2000). Seed predation rates on 13 naturalised species from 10 Asteraceae species in New Zealand are substantially lower than rates experienced by these plants in Britain, part of their native range (Fenner & Lee 2001). Interestingly, this conclusion held equally well for the three of these species from two genera that also occur in the native flora, *Senecio* and *Taraxacum*.

These findings raise the question whether native insect herbivores that could feed on naturalised plant species related to their native host plants fail to do so because they are unable to thrive in urban and rural habitats. If this were true, then biotic resistance to plant invasion provided by native insect herbivores (Mack 1996; Levine et al. 2004) could be restricted to largely intact, wild habitats and not significant in the rural and urban landscapes that now dominate New Zealand. This

could also mean that the survival and success of many monophagous native insect herbivores in modern New Zealand remain closely linked with the abundance of their native host plants and native vegetation despite the presence of congeneric naturalised potential host plants in surrounding rural and urban habitats.

We tested these ideas with the monophagous insect herbivore fauna of Auckland *Senecio* species. New Zealand has 33 wild *Senecio* species, comprised of 13 endemics, 6 native non-endemics, and 14 fully naturalised exotic species (Webb et al. 1988). Mainland Auckland includes at least 19 of these species (2 endemic, 6 native, 11 naturalised). New Zealand *Senecio* are fed upon by a variety of native and naturalised insect species of varying degrees of host specialisation (Spiller & Wise 1982), including the following wholly or largely genus-specific endemic species: *Nyctemera annulata* (Boisduval, 1832) (Lepidoptera, Arctiidae, the New Zealand magpie moth), *Patagoniodes farnaria* (Turner, 1904) (Lepidoptera, Pyralidae), *Stigmella ogygia* (Meyrick, 1889b) (Lepidoptera, Nepticulidae), and *Tephritis fascigera* Malloch (Diptera, Tephritidae).

In Australia, the native *Nyctemera amica* (now naturalised in New Zealand and hybridising with *N. annulata*; see Kay 1980) preferred and performed better on the Australian native *Senecio pinnatifolius* than on the naturalised *S. madagascariensis* (White et al. 2008a; see also White et al. 2008b). While White et al. (2008a) interpreted this as supporting the enemy release hypothesis, their lack of replication of native and naturalised species makes this conclusion tentative.

In our study, we sought to answer two questions. To what extent do endemic monophagous insect herbivores of *Senecio* occur in modified rural and urban habitats in Auckland? To what extent do these herbivores feed on naturalised *Senecio* species?

Methods

Species

We used observations and experiments to document the host associations and habitat preferences of three widespread native monophagous insects that feed on above-ground vegetative tissue of *Senecio*: *Nyctemera annulata*, *Patagoniodes farnaria*, and *Tephritis fascigera*. The leaf mines of the endemic *S. ogygia* can be confusingly similar to the mines of the naturalised European fly, *Chromatomyia syngenesiae* (Diptera, Agromyzidae), which is now abundant on *Senecio* and other Asteraceae in New Zealand (Spiller & Wise 1982). We did not reliably distinguish leaf mines of these two species early in this study and so are unable to present quantitative information on *Stigmella ogygia*.

We examined the presence of these three herbivores on *Senecio* species occurring in Auckland: the native

species *S. glomeratus*, *S. hispidulus*, and *S. minimus* and the non-native naturalised species *S. bipinnatisectus*, *S. diaschides*, *S. esleri*, *S. jacobaea*, *S. skirrhodon*, and *S. vulgaris*. We failed to find any individuals of two endemics, *S. rufiglandulosus* and *S. scaberulus* (the former was last collected near Whatipu Beach, Waitakere Ranges, in 1993 (Auckland Herbarium AK 209903), and the latter at Papanui Point of the Hunua Ranges, in 1983 (AK 165332)). Plant names follow the New Zealand Plant Names Database (<http://nzflora.landcareresearch.co.nz/>).

Field survey

Our observations were made from plants collected between December 2001 and April 2002, when we bagged and collected whole plants of all of the above species. Our intention was to collect from each species ten randomly selected plants from each of five sites from each of two broad habitat types: wildland (typically native forest tracksides, streamsides, and other forest edges) and rural/urban (rural was restricted to pastoral landscapes and urban comprised private gardens, open parkland, roadsides, and grass-dominated urban wastelands). All wildland sites were within the Waitakere Ranges, the Hunua Ranges, Long Bay Regional Park, and native forest within the Woodhill plantation (except Murphy's Bush, Otara). Rural/urban sites were in Auckland City, Waitakere City, and in rural areas between Auckland City and the Waitakere Ranges, Hunua Ranges, and Long Bay Regional Park.

We could not follow this plan because of the scarcity (perhaps absence) of some species in some landscapes, combined with our need to make all collections within one growing season. Instead, up to 10 large (non-seedling) plants were collected of the following species: *Senecio bipinnatisectus* (4 rural/urban sites, 5 wildland sites), *S. diaschides* (2 wildland sites), *S. esleri* (2 rural/urban site, 3 wildland sites), *S. glomeratus* (5 wildland sites), *S. hispidulus* (1 rural/urban site, 5 wildland sites), *S. jacobaea* (6 rural/urban sites, 8 wildland sites), *S. minimus* (3 wildland sites), *S. skirrhodon* (4 rural/urban sites, 3 wildland sites), *S. vulgaris* (4 rural/urban sites, 1 wildland sites) (Table 1).

With the exception of the removal of some juvenile invertebrates for rearing, all bagged plants were placed in the freezer less than 48 h after collection, and were later dissected and searched for all insects and insect herbivore damage. We recorded the number of individuals of *Nyctemera* spp., *Patagoniodes farnaria*, and *Tephritis fascigera*, as well as all other herbivorous insects and insect herbivore damage. The endemic *N. annulata* now readily hybridises throughout Auckland with the naturalised Australian congener *N. amica*, the other *Nyctemera* species in New Zealand (Kay 1980). We observed wide variation in larval hairs consistent with hybridisation and therefore refer to *Nyctemera* spp. throughout the rest of this paper.

Table 1. Mean (\pm SE) proportion of plants in each habitat type of each *Senecio* species, containing one of three endemic, monophagous *Senecio* herbivores. *Senecio* species are listed in descending order of the cumulative proportion of plants containing herbivores. Sites are separated into wildland and rural/urban (labelled 'rural' in the table, since the majority of these sites were rural). *Nyctemera* larvae in Auckland are a combination of the endemic *N. annulata*, the naturalised Australian *N. amica*, and hybrids of the two. *Senecio* species include native ('Nat') and naturalised ('Ex') species.

<i>Senecio</i> spp.	Number plants (sites)		<i>Nyctemera</i> spp.		<i>Patagoniodes farnaria</i>		<i>Tephritis fascigera</i>	
	Rural	Wild	Rural	Wild	Rural	Wild	Rural	Wild
<i>S. esleri</i> (Ex)	15(2)	30(3)	0	0.10(0.06)	0	0.07(0.05)	0.27 (0.12)	0.30(0.09)
<i>S. jacobaea</i> (Ex)	51(6)	81(8)	0.29(0.06)	0.20(0.04)	0.04(0.03)	0.06(0.03)	0.06(0.03)	0
<i>S. minimus</i> (Nat)	-	21(3)	-	0.14(0.08)	-	0.24(0.10)	-	0.24(0.10)
<i>S. skirrhodon</i> (Ex)	27(4)	30(3)	0.04(0.04)	0.07(0.05)	0.04(0.04)	0.07(0.05)	0.11(0.06)	0.13(0.06)
<i>S. bipinnatisectus</i> (Ex)	40(4)	43(5)	0.02(0.02)	0.16(0.06)	0	0.05(0.03)	0	0.07(0.04)
<i>S. diaschides</i> (Ex)	-	16(2)	-	0	-	0	-	0.19(0.10)
<i>S. hispidulus</i> (Nat)	1(1)	45(5)	0	0	0	0.02(0.02)	0	0.11(0.05)
<i>S. vulgaris</i> (Ex)	36(4)	10(1)	0.08(0.05)	0	0	0	0	0
<i>S. glomeratus</i> (Nat)	-	19(5)	-	0.05(0.05)	-	0	-	0

Field experiment

We complemented our observations with a pot experiment using plants growing from seed of *Senecio bipinnatisectus*, *S. hispidulus*, *S. jacobaea*, and *S. minimus*. Seed was germinated in a glasshouse over the summer of 2003/04 and seedlings were planted out at the beginning of May 2004, with three seedlings planted in each 1-L pot, later thinned to a single plant per pot. Pots were filled with local soil from each site. One pot of each species was placed among 12 soil-filled pots tightly packed into polystyrene trays lined with water-absorbent capillary matting. Each tray was connected to a drip watering system set on a timer to ensure the pots did not dry out. Six replicate trays were laid out at each of five sites: Long Bay Regional Park ranger depot, Cascades Kauri Regional Park ranger depot, Arataki storage depot (Waitakere Ranges Regional Park), Chris Winks's home in Tamaki (Ropata Ave), and the Mount Albert Research Centre (Auckland). The first two sites are surrounded by native forest, the Long Bay site is between native forest and rural farmland, and the latter two sites are urban. There were wild *Senecio* species present at all sites, although we did not note the species present or their relative abundances.

The experiment was harvested mid-March 2005, when the plants were comprehensively searched for insects and insect herbivore damage. Each plant was scored for percentage leaf loss into the categories 0–5%, >5–10%, >10–25%, >25–50%, >51–75%, >76–100%. For each plant we also recorded its height, reproductive status, and dry above-ground mass. A pilot study of the same experiment, with *Senecio hispidulus* and *S. jacobaea*, and *S. rufigliandulosus* (from Taranaki seed), was set up with seed planted in July 2003 and was harvested at the same time as the full experiment. These experiments were part

of a larger project in both Auckland and Christchurch that included additional trays of plants that received insecticide and fungicide treatments. Only the control plants are reported on here.

Statistical analysis

Both datasets were analysed with binomial generalised linear models (quasi-binomial when necessary) using R version 2.2.1 (R Development Core Team 2005). The response variable was a two-column matrix of the number of plants with and without a herbivore species, per site and species. Explanatory variables were the species and habitat type (wildland or rural/urban). In the case of the survey data, the sum of the heights of all plants of a species at a site was used as a covariate to capture any effect of variation in plant size among species and sites. For the experimental data, we summed dry mass at harvest as a more accurate measure of plant size. In the experimental dataset, orthogonal contrasts within species were used to compare naturalised with native species and to compare the species within those categories.

Results

Field survey

The endemic insects occurred on naturalised *Senecio* species as often as on native ones (Table 1). In the field survey, of our three focal herbivores, *Nyctemera* spp. and *Tephritis fascigera* showed significant variation among *Senecio* species (*Nyctemera* spp.: quasi-binomial GLM, $P < 0.01$, d.f. = 8, for the minimum adequate model with species and plant height; *T. fascigera*: $P < 0.05$, d.f. = 8, for the minimum adequate model with species). The

highest *Nyctemera* spp. abundance was on the naturalised ragwort, *Senecio jacobaea* (23% of all plants sampled had at least one larva, $N = 132$), followed by the native *S. minimus* (14% of plants, $N = 21$), and the naturalised species *S. bipinnatisectus* (10%, $N = 83$) and *S. esleri* (7%, $N = 45$). *Nyctemera* spp. was not found on the naturalised *S. diaschides* or the native *S. hispidulus* (we have at other times observed *Nyctemera* feeding on both species).

The highest *Tephritis fascigera* abundance was on the naturalised *Senecio esleri* (29% of plants, $N = 45$), followed by the native *S. minimus* (24% of plants, $N = 21$), and the naturalised *S. diaschides* (19%, $N = 16$). For both *Nyctemera* spp. and *Tephritis fascigera* occurrence, a priori contrasts found no significant difference between naturalised and native hosts.

In the field survey, none of the three focal herbivore species showed a statistically detectable response ($P < 0.05$) to our two habitat classes, wildland and rural/urban, although all three herbivores had their highest abundance in wildlands (Table 1).

Field experiment

The patterns obtained were similar to, but typically stronger than, those of the field survey (Table 2). *Tephritis fascigera* galls were only found on *Senecio minimus* plants and only at wildland sites (all three sites), corresponding to a significant effect of species ($P < 0.001$, d.f. = 3) and habitat ($P < 0.001$, d.f. = 1, with no significant contribution of plant mass).

Tephritis fascigera in *Senecio bipinnatisectus* galls found in the field survey were typically associated with the stems of the inflorescences of large plants, rather than the main stem. Most experimental *S. bipinnatisectus* plants were flowering and/or seeding when harvested, but they were shorter (mean height $28.4 \text{ cm} \pm 5.2 \text{ SE}$) than the largest wild plants that reach $>100 \text{ cm}$. Of the surviving 2-year-old plants of *S. hispidulus* (20 urban plants and 17 wildland plants) and *S. jacobaea* (one urban and three rural) from the pilot study, none had *Tephritis fascigera* galls.

Larvae of *Patagoniodes farnaria* were only found on *Senecio jacobaea* and *S. minimus*, at one wildland site (Cascades Kauri Park, only on *S. jacobaea*) and one urban site (Tamaki, on both species) (Table 2). Bores were significantly more likely on *S. minimus* than *S. jacobaea* plants ($P < 0.05$, d.f. = 3, with no significant contribution of plant mass) although there was no significant effect of habitat. Of the surviving 2-year-old plants of *S. hispidulus* and *S. jacobaea* from the pilot study, none had *P. farnaria* bores.

No *Nyctemera* spp. larvae were found on the plants at harvest on either the 10-month or 2-year-old plants. Although we did observe *Nyctemera* larvae on non-experimental *Senecio* in March 2005 (when the experiment was harvested), it is likely that many, perhaps most, of the *Nyctemera* larvae active during the summer had pupated by this time. *Nyctemera* spp. activity can be gleaned from the degree of folivory, since *Nyctemera* larvae are the most abundant folivore we observed on *Senecio* in Auckland (unpubl. data).

For each species, there was the same or a greater proportion of plants with $>5\%$ leaf area loss at wildland than urban sites (habitat effect $P < 0.001$, d.f. = 1) and there were significant differences among species (species effect $P < 0.001$, d.f. = 3, with no significant contribution of plant mass) (Table 2). Folivory was higher on the naturalised than the native species ($P < 0.05$) and, of the naturalised species, *Senecio jacobaea* had higher folivory than *S. bipinnatisectus* ($P < 0.001$). The difference in folivory between the native *S. minimus* and *S. hispidulus* was not significant.

Similar differences in folivory were found on the 2-year-old plants. At the urban sites, 11% of plants had $>5\%$ folivory ($N = 18$ surviving plants) and 32% at the wildland sites ($N = 24$) ($P < 0.05$, d.f. = 1). There was significant variation among species ($P < 0.05$, d.f. = 2, with no significant contribution of plant mass). Again, folivory on the naturalised species, *S. jacobaea*, was higher (4 of the 5 surviving plants with $>5\%$ folivory) than on the natives, in this case *S. hispidulus* (4 of 32 plants) and *S. rufiglandulosus* (2 of 5 plants) ($P < 0.05$).

Table 2. Proportion of plants (mean \pm SE) with larvae or characteristic damage from two endemic, monophagous *Senecio* herbivores, on four *Senecio* species (native, 'Nat', and naturalised, 'Ex') experimentally grown at five sites in Auckland (six plants per site, two urban sites and three wildland sites) over 10 months. Species sequence is by the decreasing level of herbivory in wild habitats.

<i>Senecio</i> spp.	$>5\%$ folivory		<i>Patagoniodes farnaria</i>		<i>Tephritis fascigera</i>	
	Urban	Wild	Urban	Wild	Urban	Wild
<i>S. jacobaea</i> (Ex)	0.58(0.15)	0.89(0.08)	0.17(0.11)	0	0	0
<i>S. minimus</i> (Nat)	0.08(0.08)	0.61(0.12)	0.33(0.14)	0.17(0.09)	0	0.56(0.12)
<i>S. bipinnatisectus</i> (Ex)	0.08(0.08)	0.38(0.12)	0	0	0	0
<i>S. hispidulus</i> (Nat)	0.17(0.11)	0.33(0.11)	0	0	0	0

Other herbivorous insects

At the time of our study, the pasture weed ragwort, *Senecio jacobaea*, had three carefully selected monophagous biological control agents released on it in New Zealand: *Botanophila jacobaea* (Diptera, Anthomyiidae, synonym *Pegohylemyia jacobaeae*), *Longitarsus jacobaeae* (Coleoptera, Chrysomelidae, the ragwort flea beetle), and *Tyria jacobaeae* (Lepidoptera, Arctiidae, the cinnabar moth) (Syrett et al. 1991). We collected two of these agents on *S. jacobaea* in Auckland. *Tyria jacobaeae* larvae were collected on *S. jacobaea* at Dome Valley, Warkworth, a release site (although not from on our 10 survey plants). No *Longitarsus jacobaeae*, adults or larvae, were found in the survey plants, although small scraped holes on the leaves of *S. jacobaea*, consistent with adult feeding, were found on the Panto Track in the south of the Waitakere Ranges, one of our wildland survey sites. In the experiments, two *L. jacobaeae* adults were found on two 2-year-old *S. jacobaea* plants at Long Bay and one adult on a 10-month-old *S. jacobaea* at Arataki. No individuals or damage of any biocontrol agent were seen on any other *Senecio* species in this project (this included 10 *S. bipinnatisectus* plants we collected at Dome Valley).

Discussion

Our results show that *Nyctamera annulata*, *Patagoniodes farnaria*, and *Tephritis fascigera*, three endemic monophagous insect herbivores of *Senecio*, all occur in modified rural and urban habitats in Auckland and feed on naturalised *Senecio* species. Therefore, to some degree, their abundance is likely disconnected from the abundance of their native *Senecio* hosts. From the perspective of conserving New Zealand's endemic biodiversity, this is important, as it means these herbivores have likely been little affected by the alarming decline in abundance of *S. rufigliandulosus* and *S. scaberulus* in Auckland, and the scarcity of natives like *S. glomeratus*, *S. minimus*, and *S. quadridentatus* in rural and urban Auckland compared with common naturalised species (JJS, pers. obs.).

Each of these insect species exhibited host plant preferences, but this did not usually follow our human dichotomy of naturalised versus native species. Indeed, the pasture weed ragwort, *Senecio jacobaea*, appears to be an acceptable host plant of all three insect species, with *Nyctamera* most frequently collected on *S. jacobaea*. Similarly, *Tephritis fascigera* was most frequently collected on the naturalised *S. esleri*. The native *S. minimus* was always a preferred host plant for all three species, with *Patagoniodes farnaria* most frequently collected on *S. minimus*. These results suggest that there is no general rule that endemic insects are best adapted to feed on their original, native host species. This finding contradicts the conclusions of (White et al. 2008a), although these were based on only one naturalised and one native (*Senecio*) species.

The four *Senecio* species we most commonly encountered in Auckland, especially in urban and rural areas, were *S. bipinnatisectus*, *S. esleri*, *S. hispidulus*, and *S. vulgaris* (listed in alphabetical order). Each is a naturalised species, with the exception of *S. hispidulus*, which now contains a widespread, naturalised Australian glabrescent form (P. J. de Lange, Department of Conservation, Auckland, pers. comm.).

While these insects did not show a preference for their original, native, host plants, all tended to be more common in forested wildland habitats. This is consistent with earlier results from other New Zealand insect taxa (Kuschel 1990; Harris & Burns 2000; Derraik et al. 2005), although the *Senecio* herbivores do not show the extreme degree of habitat specialisation that Kuschel (1990) found for herbivorous beetles in Lynfield, Auckland.

The abundance and distribution of our three endemic insect herbivores would be substantially reduced and concentrated in wildlands in Auckland were it not for the presence of these naturalised *Senecio* species. It would be worth checking if this pattern is widespread in the New Zealand insect herbivore fauna, because at least 99 naturalised plant genera in New Zealand (13% of all naturalised plant genera) have native congeners (Duncan & Williams 2002). Likewise, it would be worth exploring how widespread is the pattern of herbivorous native insects preferring wildland habitats (Kuschel 1990; Harris & Burns 2000). Both patterns have important implications for such diverse issues as habitat restoration, biotic resistance to plant invasions, and the response of herbivorous insect populations to climate change in the fragmented and modified landscapes that dominate lowland New Zealand.

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