Distribution and abundance of endemic coelostomidiid scale insects (Hemiptera: Coelostomidiidae) in Auckland forests, New Zealand

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Abstract: Sap-feeding insects can excrete considerable quantities of sugar-rich honeydew. In New Zealand, South Island beech (*Nothofagus* spp.) forests are shaped by the extensive honeydew resource produced by two endemic coelostomidiid species (*Ultracoelostoma assimile* and *U. brittini*) and geckos on northern islands are known to feed on the honeydew of a third endemic coelostomidiid, *Coelostomidia zealandica.* There are six other endemic coelostomidiid species in New Zealand that utilise a range of plant hosts but the ecological role of these species is poorly understood. A survey of mainland forests in the Auckland Ecological Region was conducted in February–April 2006 to investigate the distribution and abundance of coelostomidiids in this area. Three coelostomidiid species were detected in the survey (*C. zealandica*, *C. pilosa* and *C. wairoensis*) and five new host–scale insect associations were identified. *C. zealandica* was uncommon, *C. pilosa* was widespread in broadleaved–podocarp forest but only formed light infestations, and *C. wairoensis* was present in all teatree stands examined, often forming heavy infestations on kānuka (*Kunzea ericoides*). Infested kānuka trees had sooty moulds growing on them and exotic wasps were regularly seen feeding on *C. wairoensis* honeydew. The extent and intensity of *C. wairoensis* infestation on kānuka suggests it will have community-level impacts.

Keywords: *Coelostomidia,* honeydew, insect herbivory, *Ultracoelostoma*

Introduction

Sap-feeding Hemiptera typically excrete a mixture of water, sugar and amino acids known as 'honeydew' and when sap-feeders are abundant they can release copious amounts of honeydew onto leaf surfaces, litter and soil. The presence of this sugar-rich resource can affect community functioning at various levels. For example, in German spruce forests extensive aphid infestations are common and, although each aphid produces only approximately 0.2 mg dry mass of honeydew per day, annual honeydew production can be up to 60 kg per tree (Muller 1956, cited in Stadler et al. 1998). Phyllosphere microorganisms respond positively to the honeydew and population densities of leaf moulds, yeasts and bacteria can be two to three orders of magnitude higher on infested than uninfested spruce (Stadler & Mueller 1996; Stadler et al. 1998). Rain that has passed through the canopies of infested spruce contains higher amounts of dissolved carbon while soils beneath infested spruce can show seasonal reductions in nitrogen levels compared with uninfested spruce (Stadler et al. 1998; Michalzik et al. 1999).

In New Zealand, two honeydew-producing scale insect species in the Coelostomidiidae family (*Ultracoelostoma assimile* (Maskell, 1890) and *U. brittini* Morales, 1991; known as sooty beech scales) are relatively well researched as they infest extensive areas of beech (*Nothofagus* spp.)[1] forest in the South Island. The Coelostomidiidae family consists of 14 species: five in the Neotropical genera *Cryptokermes, Mimosicerya* and *Paracoelostoma*, six in the endemic New Zealand genus *Coelostomidia*, and three in the endemic New Zealand genus *Ultracoelostoma* (Gullan & Sjaarda 2001; Hodgson & Foldi 2006; Gullan & Cook 2007; Miller et al. 2007). Like other members of the coelostomidiid family, the beech *Ultracoelostoma* species excrete honeydew via a waxy anal tube and it is estimated that *Ultracoelostoma* produce up to 3500–4500 kg dry weight honeydew per hectare annually in the southern beech forests (Beggs et al. 2005). This year-round source of sugar is extensively utilised by birds, fungi, and invertebrates (Ewers 2002; Beggs et al. 2005; Beggs & Wardle 2006). The beech *Ultracoelostoma* species are regarded as keystone species because of the extent of their honeydew production and its impact on forest community structure (Beggs & Wardle 2006).

Another endemic coelostomidiid, *Coelostomidia zealandica* (Maskell, 1880), may also play a significant

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[1] Plant names follow Allan Herbarium (2000)

ecological role in New Zealand forests. Current understanding of *C. zealandica* ecology is based largely upon observations made on Korapuki Island (Mercury Group, east of Coromandel Peninsula), a small (18 ha) modified island being restored by the Department of Conservation. Since the eradication of rats and rabbits in 1987 there has been strong regeneration of coastal forest on Korapuki Island and heavy infestations of *C. zealandica* have developed on the trunks of many karo (*Pittosporum crassifolium*) and ngaio (*Myoporum laetum*) trees in the regenerating forest (Towns 2002). Coelostomidiid-infested trees became coated with a black fungal complex (sooty mould) and geckos have been observed aggregating on infested trees and feeding on *C. zealandica* honeydew (Towns 2002). It has been suggested that, prior to human disturbance, *C. zealandica* (and other coelostomidiid species) may have been an important component of the forest communities on northern offshore islands, providing a food resource for birds, insects and reptiles (Towns 2002; Towns et al. 2003; Towns & Atkinson 2004).

There are six other coelostomidiid species in New Zealand although little is known of them, beyond basic location and host records (Table 1); but see Morales (1991) for life cycle of *Coelostomidia wairoensis* (Maskell, 1884). Location records indicate that these coelostomidiid species occur on all the main islands in New Zealand (North, South, Stewart and Chatham islands) with one species, *Ultracoelostoma dracophylli* Morales, 1991*,* also occurring on the subantarctic Auckland Islands (Morales 1991). Most are host-specific, restricted to one or few plant families but two species, *C. pilosa* (Maskell, 1891) and *C. jenniferae* Morales, 1991, are polyphagous like *C. zealandica* (Table 1; Morales 1991). Existing information therefore suggests that honeydew-producing coelostomidiids are likely to occur in a wide range of vegetation types, raising the possibility that many ecosystems in New Zealand may be influenced by honeydew.

In order to gather more information about coelostomidiids in the Auckland Ecological Region (ER), we conducted a survey of forests from February to April 2006. The main aim of the survey was to determine coelostomidiid abundance and diversity in three common forest types (mixed broadleaved–podocarp, teatree, coastal). We also recorded host information (diversity and abundance) to aid interpretation of the coelostomidiid distribution patterns. Finally, to gain preliminary information about the possible influence of honeydew in these forest types we recorded the occurrence of three known honeydew consumer groups (sooty moulds, ants and introduced *Vespula* wasps) at all forest sites.

Methods

Three forest types were included in the survey: (1) mixed broadleaved–podocarp forest; (2) teatree forest dominated by mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*); and (3) coastal forest with emergent pohutukawa (*Metrosideros excelsa*). We examined five sites for each forest type (Fig. 1). The sites were all in reserves or public parks, and were selected to provide adequate geographic coverage of the Auckland ER. To ensure samples from each site were reasonably representative, we made observations in 10 circular plots at each site, and averaged plot data to provide a single measure per site. Each plot had a 5-m radius and the plots were located at 25-m intervals along a haphazardly placed transect. Transects were laid along the edge of teatree stands and in the interior of other forest stands.

We used published literature to ascertain the coelostomidiid species likely to occur in the Auckland ER: three species are recorded from the region (*Coelostomidia zealandica, C. wairoensis,* and *C. pilosa*), and a fourth (*Ultracoelostoma assimile*) was considered likely to occur as it has been recorded from Northland and Waikato (Morales 1991). We also used published literature to develop a list of all known hosts of these four coelostomidiid species (Morales 1991; Towns 2002).

Table 1. Location and host records for *Ultracoelostoma* and *Coelostomidia* species in New Zealand. Data from Morales (1991). Abbreviations: N = North Island, S = South Island, St = Stewart Island, Ch = Chatham Islands, O = other islands, × = species recorded from location.

Species	Location records					Recorded hosts (plant families)
	N	S	St	Ch	O	
C. deboerae	×	×				Podocarpaceae
C. jenniferae		×	×	×		Many
C. montana		×				Epacridaceae
C. pilosa	×	×				Podocarpaceae and many others
C. wairoensis	×	×				Myrtaceae
C. zealandica	×	×				Many
U. assimile	×	×				Nothofagaceae, Monimiaceae and Cunoniaceae
U. brittini		×				Nothofagaceae
U. dracophylli	×	×	×	×	×	Epacridaceae

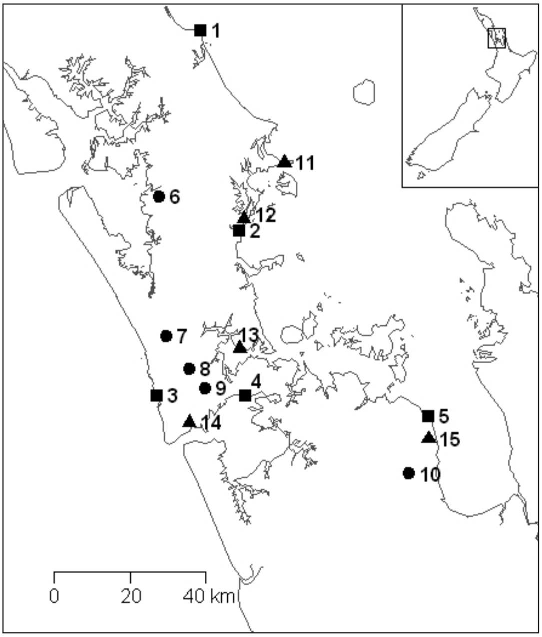

Figure 1. Study site locations. Key to symbols: ■ = Coastal forests, ● = Mixed broadleaved–podocarp forests, ▲ = Teatree forest. Key to coastal forests: 1 Mangawhai Heads, 2 Wenderholm Regional Park, 3 Piha (Waitakere Ranges Regional Park), 4 Waikowhai Reserve, 5 Tapapakanga Regional Park; Mixed broadleaved–podocarp forests: 6 Mt Auckland, 7 Huapai Reserve, 8 Swanson Reserve, 9 Oratia Reserve, 10 Vining Scenic Reserve; Teatree forest: 11 Tawharanui Regional Park, 12 Mahurangi Regional Park, 13 Kauri Point Centennial Park, 14 Karamatura Valley (Waitakere Ranges Regional Park), 15 Waharau Regional Park.

An initial pilot study detected coelostomidiids on four additional hosts and these were added to the host list (see Results for details of these new host records). We used the resulting list of 42 host species in the field to help focus searching and to gather data on host diversity, abundance, and infestation rates in the different forest types.

In each survey plot we counted all hosts (i.e. we recorded the number of plants present for each of the plant species listed as a known coelostomidiid host) and individually examined each host plant to determine if coelostomidiids or sooty mould growths were present. To allow rapid and consistent searching, a standardised approach was used. Sooty mould infestation was determined by examining hosts for black fungal growth on trunk and branches. Sooty mould presence/absence on canopy branches was estimated from the ground by eye. Coelostomidiid infestation was determined by examining the trunk of each host tree to a height of 1.3 m, and a tree was considered to be infested if the anal tube of at least one coelostomidiid was visible.

Mānuka and kānuka trees had to be treated separately however, as *Coelostomidia wairoensis* infests the branches of these hosts, rather than the trunks. To determine coelostomidiid infestation on mānuka and kānuka we examined four branchlets on each tree and the presence or absence of anal tubes was recorded. Branchlet diameters were typically 7.5–10 mm, and branchlet length was approximately 0.75 m. For tall kānuka and mānuka with inaccessible branches we estimated coelostomidiid infestation from sooty mould presence, based on the following observations. A random sample of 100 accessible mānuka and kānuka indicated that 99% of coelostomidiid infestations were accompanied by sooty mould infestation, and that 52% of kānuka with sooty mould and 9% of mānuka with sooty mould had coelostomidiid infestations. Hence in each plot we estimated coelostomidiid infestation on inaccessible kānuka and mānuka by multiplying the number of inaccessible kānuka and mānuka with visible sooty mould on trunk or branches by 0.53 or 0.09, respectively. For vines and creepers we examined the accessible portions of the plants for coelostomidiids and sooty mould, but made no attempt to count the number of plants present. Host seedlings and saplings (trunk diameter < 2.5 cm at 1.3 m) were not counted or examined.

We made more detailed observations on focal host species in each forest type. In mixed broadleaved–podocarp and teatree forests we selected four abundant and widespread host species as focal hosts (based on pilot study data). These were rimu (*Dacrydium cupressinum*) and tanekaha (*Phyllocladus trichomanoides*) in the broadleaved–podocarp forest, and mānuka and kānuka in teatree forest. In coastal forest, the focal hosts were karo and ngaio. These hosts were selected as they occur in coastal forest and because heavy coelostomidiid infestations had been recorded previously on these two species (Towns 2002). Ten haphazardly selected specimens of the two relevant focal host species were examined at each site.

On each focal tree (except mānuka and kānuka) we estimated the density of trunk-feeding coelostomidiids (anal tubes m^{-1}) by counting the number of anal tubes visible on the trunk from the ground to a height of 1.3 m and then dividing the count by the trunk surface area examined. Area was estimated as 1.3 m × trunk circumference at 1.3 m. Density estimates for mānuka and kānuka proved difficult to obtain as time constraints meant that branchlet surface area could not be measured. It was also not possible to make rapid accurate field estimates of the number of anal tubes on branchlets of heavily infested kānuka (six of the 30 focal kānuka examined during the study period, February–April 2006). However, we examined 25 heavily infested kānuka trees in the Karamatura Valley between February and early May 2008 and estimated the number of anal tubes on the main stem of one branchlet on each tree. The mean number of anal tubes per branchlet main stem was 107 (± 16 SE), and this figure was used as a branchlet estimate for the six heavily infested focal kānuka in the survey. In addition, for the Karamatura Valley kānuka we counted the number of honeydew droplets on each branchlet main stem and recorded the main stem length, minimum diameter and maximum diameter, enabling surface area to be calculated. These data were used to estimate anal tube and honeydew droplet densities for *Coelostomidia wairoensis* on the Karamatura Valley heavily infested kānuka.

We also recorded the occurrence of ants, *Vespula* wasps, and sooty mould for all focal trees. Ant and *Vespula* wasp presence/absence were determined by instantaneous scans of trunk and lower branches. If ants or wasps were present, behaviour was observed for one minute and recorded. In addition ants were collected whenever they were observed in association with coelostomidiids, other scale insects, or sooty mould in the survey plots. Collected ants were later identified in the laboratory using the key provided by Harris (2006; http://www.landcareresearch.co.nz/research/biocons/invertebrates/ants/key/). We recorded sooty mould growth on focal host trunks (to 1.3 m) and upper trunk/branches (above 1.3 m) using a scale of 0–4 (0 = no sooty mould, 1= <25% area covered by sooty mould, 2 = 25–49% cover, 3 = 50–74% cover, 4 = >75% cover). Sooty mould cover on the ground (1-m radius around trunk of each focal host) was also estimated using the same scale.

We collected coelostomidiid samples from at least one individual tree of each infested host species at each site then slide-mounted them and identified samples using keys in Morales (1991). Wherever possible at least two coelostomidiids were collected from each host sampled. There are only five hosts (*Rubus australis*, *Pseudopanax* spp., *Nothofagus solandri, N. menziesii, Metrosideros* spp.) in the Auckland ER known to be used by more than one of the Auckland coelostomidiid species (Morales 1991). Of these hosts, three were not encountered at the survey sites and one (*Pseudopanax* spp.) occurred at survey sites but was never infested. The remaining host (*Metrosideros* spp.) was widespread but was almost never infested; one coelostomidiid specimen was found on one pohutukawa tree, but unfortunately it was not able to be identified to species level. Existing literature (Morales 1991) suggests all other hosts in the Auckland ER are only used by one coelostomidiid species and this was supported by our sampling. All host species that were frequently infested were sampled more than once and there was no evidence of either mixed coelostomidiid populations on individual trees or of more than one coelostomidiid species using a host. For example, over 50 individual coelostomidiids were collected from 17 different kānuka trees at eight different sites. These were mounted and all were identified as *Coelostomidia wairoensis*. For the purposes of this paper it was therefore assumed that all coelostomidiids present on a single host plant were the same species.

Data analysis

The survey yielded data in the form of mean number of hosts per plot. To improve interpretability, data were scaled up to hosts ha^{-1}. However, as species counts are sensitive to sampling area, host diversity (total number of host species recorded in all 10 plots at each site) was not scaled up. The response variables examined were therefore host diversity, the number of hosts per hectare, the number of coelostomidiid-infested hosts per hectare, and the number of sooty-mould-infested hosts per hectare. The explanatory variable was forest type (a fixed factor with three levels) and differences between forest types were analysed using one-way ANOVA. The first three response variables were normally distributed with equal variances and were not transformed. However, the sooty-mould-infested host data were log(y + 1)-transformed prior to analysis in order to meet model assumptions. Analyses were carried out using the statistical software R.2.6.0 (R Development Core Team 2007). Means are reported with one standard error.

Results

Coelostomidiids and their hosts

Three coelostomidiid species were detected in the survey: *Coelostomidia pilosa, C. wairoensis* and *C. zealandica* (see Table 2 for host records for each species). *C. pilosa* was detected at all broadleaved–podocarp forest sites and in these forests *C. pilosa* feeding stages were found on six conifer species including three new host records: manoao (*Halocarpus kirkii)*, kahikatea (*Dacrycarpus dacrydioides)* and tanekaha. *C. pilosa* was also found on hard beech (*Nothofagus truncata*), a new host record for the species. The plot survey detected *C. zealandica* at only one coastal forest site where it was feeding on karo. However, additional hand searching detected *C. zealandica* on mamangi (*Coprosma arborea*, new host record) in an inland broadleaved–podocarp forest. *C. wairoensis* feeding stages occurred predominantly on kānuka and *C. wairoensis* was detected at all sites where accessible kānuka trees were present. *C. wairoensis* infestation on mānuka was rare (not detected in any plots, detected three times on focal trees), but eriococcid infestation was common. Eriococcid species detected on mānuka were *Eriococcus leptospermi* Maskell, 1891, *E. campbelli* Hoy, 1959 and *E. orariensis* Hoy, 1954**.** Of these, *E. campbelli* was also detected on kānuka**.**

The mean number of hosts per hectare did not differ significantly between forests (Fig. 2, $F_{2,12} = 2.12$, $P = 0.16$), but host diversity was higher in broadleaved–podocarp forest (mean number of host species per site = 7 ± 0.55 SE) than in coastal forest (3.2 ± 0.37) or teatree forest (3.2 ± 0.80) ($F_{2,12} = 13.37$, $P < 0.001$; Tukey HSD tests: coastal vs broadleaved–podocarp $P = 0.002$, coastal vs teatree $P = 1$, broadleaved–podocarp vs teatree $P = 0.002$). The

Table 2. Coelostomidiid infestation rates on known hosts and new hosts, Auckland Ecological Region. Figures are based on data from sites where a given coelostomidiid species was detected. For host genera that included vines (e.g. *Metrosideros* spp.), the number of sites where the host co-occurred with a given coelostomidiid species is indicated along with the extent of infestation (i.e. the number of individual vines was not recorded). An asterisk indicates a new host record for a species.

Coelostomidia species	Plant hosts recorded in survey[1]	No. hosts examined	% hosts infested
C. pilosa	Conifers:		
	Kahikatea (*Dacrycarpus dacrydioides*, Podocarpaceae)*	7	71
	Manoao (*Halocarpus kirkii*, Podocarpaceae)*	3	100
	Miro (*Prumnopitys ferruginea*, Podocarpaceae)	5	80
	Rimu (*Dacrydium cupressinum*, Podocarpaceae)	29	76
	Tōtara (*Podocarpus totara*, Podocarpaceae)	12	42
	Tanekaha (*Phyllocladus trichomanoides*, Phyllocladaceae)*	133	46
	Flowering plants:		
	Freycinetia sp. (Pandanaceae)	4/5 sites	0
	Hard beech (*Nothofagus truncata*, Nothofagaceae)*	8	88
	Metrosideros spp. (Myrtaceae)	5/5 sites	0
	Pseudopanax spp. (Araliaceae)	49	0
	Rubus spp. (Rosaceae)	2/5 sites	0
	Supplejack (*Ripogonum scandens*, Smilacaceae)	2/5 sites	0
C. wairoensis	Flowering plants:		
	Kānuka (*Kunzea ericoides*, Myrtaceae)	197	21
	Mānuka (*Leptospermum scoparium*, Myrtaceae)	125	0.02
C. zealandica	Flowering plants:		
	Griselinia sp. (Cornaceae)	1	0
	Karo (*Pittosporum crassifolium*, Pittosporaceae)	20	40
	Mamangi (*Coprosma arborea*, Rubiaceae)*	11	27
	Pseudopanax spp. (Araliaceae)	20	0

[1] Terminology follows Allan Herbarium (2006).

mean number of coelostomidiid-infested hosts per hectare also differed between forest types (Fig. 2; $F_{2,\,12} = 5.72$, $P = 0.02$), with fewer infested hosts in coastal forests than in broadleaved–podocarp forest (Tukey HSD tests: coastal vs broadleaved–podocarp $P = 0.02$, coastal vs teatree $P = 0.08$, broadleaved–podocarp vs teatree $P = 0.7$).

There were conspicuous differences in coelostomidiid densities (anal tubes m^{-2}) between coelostomidiid–host combinations (Fig. 3, Table 3). *Coelostomidia zealandica* and *C. pilosa* were never detected in high densities on their hosts, whereas *C. wairoensis* formed heavy infestations with high coelostomidiid densities on some kānuka trees (Fig. 3, Table 3). The 25 heavily infested kānuka in the Karamatura Valley had on average 12 360 (± 1726 SE) anal tubes per square metre of branchlet bark. The maximum density recorded was 34 505 tubes m^{-2}. The mean density of honeydew on the same kānuka trees was 4119 (± 841 SE) droplets m^{-2}. The maximum density of honeydew recorded was 18 329 droplets m^{-2}.

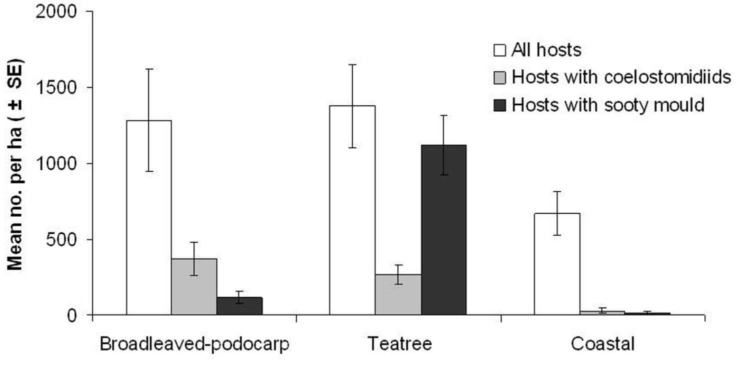

Figure 2. Number of hosts (white), coelostomidiid-infested hosts (grey) and sooty-mould-infested hosts (black) in three forest types, Auckland Ecological Region.

Table 3. Mean densities of coelostomidiid species on six focal host species. Density estimates are given for both randomly sampled hosts (i.e. uninfested hosts included in samples) and for samples of infested hosts only. Estimates are based on data from sites where the particular host-coelostomidiid combination occurred (e.g. ngaio estimate is based on data from Piha, the only survey site where *Coelostomidia zealandica* and ngaio co-occurred).

Host	Coelostomidiid	Randomly selected hosts			Infested hosts		
		Anal tubes/trunk or branchlet	Anal tubes m^{-2}	*n*	Anal tubes/trunk or branchlet	Anal tubes m^{-2}	*n*
Rimu	*C. pilosa*	1.3 ± 0.3	2.4 ± 0.6	50	3.0 ± 0.6	5.5 ± 1.1	22
Tanekaha	*C. pilosa*	3.3 ± 0.9	7.1 ± 2.0	40	6.8 ± 1.4	15.0 ± 3.5	19
Karo	*C. zealandica*	1.6 ± 1.1	6.4 ± 4.7	20	10.7 ± 5.0	42.4 ± 24.7	3
Ngaio	*C. zealandica*	0	0	5	-	-	-
Mānuka	*C. wairoensis*	0.015 ± 0.008	-	49	0.25 ± 0	-	3
Kānuka	*C. wairoensis*	14.2 ± 4.9	-	50	30.9 ± 9.7	-	23
Kānuka heavily infested with *C. wairoensis,* Karamatura Valley					-	12 360 ± 1726	25

Figure 3. *Coelostomidia pilosa* (left) in bark crevice on rimu trunk and *C. wairoensis* (right) with honeydew droplets on kānuka branches, Auckland Ecological Region.

Honeydew consumers

Blackened sooty-mould-infested trees were a noticeable feature of teatree forests and the number of sooty-mould-infested hosts was significantly higher in teatree forest than in either coastal forest or broadleaved–podocarp forest (Fig. 2; $F_{2,12} = 27.16$, $P < 0.001$, Tukey HSD tests on log(y+1) data: coastal vs broadleaved–podocarp $P = 0.81$, coastal vs teatree $P < 0.001$, broadleaved–podocarp vs teatree $P < 0.001$). Most (92%) of the focal mānuka and kānuka examined in teatree forests had some sooty mould on their branches and/or trunks, with 4% of the focal kānuka and 18% of the focal mānuka having more than half of their branches and trunk covered with sooty mould. In contrast, 12% of the tanekaha focal trees had limited sooty mould (< 25% cover) on their lower trunks, and no other focal trees in broadleaved–podocarp forest or coastal forest had sooty mould growth present. None of the focal trees in any of the forests had sooty mould growing on the ground around their trunks.

Introduced wasps, *Vespula germanica* (Fabricius, 1793) and *V. vulgaris* (Linnaeus, 1758), were recorded in instantaneous scans on three (6%) of the focal kānuka. In all three cases the kānuka trees were infested with *Coelostomidia wairoensis* and the wasps were observed feeding on honeydew droplets and searching trunk and branch surfaces. *Vespula* wasps were also recorded in instantaneous scans on seven (14%) of the focal mānuka. The wasps on mānuka were observed searching trunk surfaces and on two occasions the wasps appeared to feed on substances in bark crevices. No coelostomidiids were found on the mānuka involved, but all trees had heavy sooty mould growths and eriococcids (*Eriococcus leptospermi* and *E. orariensis*) were detected on three of the mānuka. Wasps were not observed on any other focal hosts.

Instantaneous scans detected ants on two focal karo in the coastal forest at Piha: on one tree native *Monomorium antarcticum* (Fr. Smith, 1858) ants were observed on the trunk and were also collected from *Coelostomidia zealandica* cysts on karo roots beneath leaf litter. On the other tree at Piha exotic Argentine ants, *Linepithema humile* (Mayr, 1868), were observed in and around bark crevices that contained feeding stages of *C. zealandica*. At the same site Argentine ants were also observed touching the anal area of the pseudococcid *Paracoccus glaucus* (Maskell, 1879) feeding on flax (*Phormium tenax*) and were observed travelling along sooty-mould-coated astelia (*Astelia banksii*) blades infested with the pseudococcid *Rastrococcus asteliae* (Maskell, 1884). At Waikowhai Reserve (Auckland City), Argentine ants were observed on planted mānuka infested with *Eriococcus orariensis*.

Discussion

Coelostomidiid distribution and abundance

This survey has shown that coelostomidiids are widespread across the Auckland ER: *Coelostomidia wairoensis* was detected in all teatree forests and wherever kānuka stands were present, while *C. pilosa* was detected at all broadleaved–podocarp forest sites. However, *C. zealandica* was only detected at two sites in the entire survey and the causes of this patchy distribution are unclear. *C. zealandica* is polyphagous and has been recorded feeding on 19 host species, but heavy infestations of *C. zealandica* have only been observed on ngaio and karo (Morales 1991; Towns 2002). Both ngaio and karo are known to suffer reduced recruitment in the presence of rabbits and rodents (Campbell & Atkinson 1999; Towns 2002) and although karo was abundant at some sites we found ngaio to be sparse in the region. If ngaio is a preferred host of *C. zealandica* then it is possible that reduced ngaio abundance may account for low *C. zealandica* numbers observed in our survey.

Although widespread, coelostomidiids are not equally abundant in all forest types. We found that coastal forests had fewer coelostomidiid-infested hosts than other forests and this difference may not be related simply to the availability of hosts, as total host densities did not vary significantly between forest types at our level of replication. However, host diversity was low in coastal forests and the host species present may not have been the preferred hosts of the Auckland coelostomidiids. For example, 66% of the hosts present in coastal forests were *Pseudopanax* spp. and although this species is recorded as a host for both *Coelostomidia pilosa* and *C. zealandica*, no infestation was detected on any of the 230 *Pseudopanax* specimens examined during the course of the survey. Differences in fragmentation and disturbance between forest types may also affect coelostomidiid abundance. For example, coastal forests in the Auckland ER have been extensively cleared and modified, and many remaining coastal stands are isolated fragments. Coelostomidiids may therefore find it more difficult to establish and/or survive in coastal forests than in other forest types.

At the scale of individual host trees, differences between coelostomidiid–host combinations were apparent. *Coelostomidia wairoensis* infestations on kānuka branch tips were often heavy, with anal tube densities up to 34 505 tubes per square metre recorded on branchlet stems. In contrast, both *C. pilosa* and *C. zealandica* were only observed at low densities on their hosts. Our survey recorded the number of coelostomidiids on the lower trunks of host trees (except for mānuka and kānuka), which may have underestimated infestation levels, as Wardhaugh et al. (2006) found that *Ultracoelostoma* densities were higher in the canopy branches of beech trees than on trunks. However, excluding mānuka and kānuka, we only saw scattered infestations (if any) above 1.3 m on hosts and sooty mould growth was not apparent on upper trunks and branches, suggesting that heavy coelostomidiid infestations were not present on the upper portions of the hosts. We did find, however, that both *C. pilosa* and *C. zealandica* formed infestations on host roots. These root infestations were sometimes more dense than the trunk infestations on the same tree, but were never associated with any sooty mould growth. Overall, we saw no sign of heavy *C. pilosa* or *C. zealandica* infestations in any of the Auckland forests surveyed.

Hence distribution differences are apparent at both the spatial scales examined, with teatree forest consistently having kānuka with moderate to heavy infestations, broadleaved–podocarp forest consistently having light infestations, and coastal forest occasionally having light infestations. Differences between forest types were further accentuated by widespread infestation of mānuka and kānuka by honeydew-producing eriococcids in teatree forests.

Consumer responses

This survey gathered information about three consumer groups that are commonly associated with honeydew: sooty moulds, *Vespula* wasps, and ants. Sooty moulds grow in abundance wherever sugar resources are available (Hughes 1976) and provide both shelter and food resources for an array of invertebrates (Didham 1993; Ewers 2002). In the present study, extensive sooty mould growth was observed in teatree forests where coelostomidiids and eriococcids were widespread. Sooty mould growths were not common in coastal or broadleaved–podocarp forests.

Vespula wasps (*V. germanica* and *V. vulgaris*) have invaded South Island beech forests where they dominate the honeydew resource for a portion of each year and exert considerable predation pressure on other forest invertebrates (Beggs 2001). These exotic wasp species are common throughout New Zealand and, although only occasionally detected in instantaneous scans, *Vespula* wasps were regularly observed feeding on *Coelostomidia wairoensis* honeydew in the teatree forests visited during our survey. Subsequent research in the Karamatura Valley (Waitakere Ranges, Auckland) has confirmed that *Vespula* wasps are the dominant diurnal consumer of kānuka honeydew in this area (Gardner-Gee & Beggs in press; R Gardner-Gee unpubl. data). *Vespula* wasps were also plentiful at several of the broadleaved–podocarp forest sites surveyed. *C. pilosa* was present at these sites but no honeydew feeding or wasp–coelostomidiid interactions were observed, presumably because honeydew is a sparse resource that is not profitable to harvest in broadleaved–podocarp forest.

Ant activity was not conspicuous except where Argentine ants were present. Although specific feeding behaviour was not observed, Argentine ants were found in numbers on four native plants species each infested with a different hemipteran species. Three of the hemipteran species were native, while the fourth (*Eriococcus orariensis*) was introduced from Australia in the 20th century (Hoy 1961). Argentine ants have been observed tending a wide variety of hemipteran species on horticultural crops in New Zealand (Lester et al. 2003) and the associations reported here suggest that Argentine ants may opportunistically utilise hemipteran species on native hosts as well. Little is currently known about the impacts of exotic ants on New Zealand native forest systems, but international evidence suggests that honeydew resources may facilitate exotic ant establishment and exacerbate the impacts of exotic ants on native ecosystems (O'Dowd et al. 2003).

Comparisons with previous research

The distribution patterns observed in this study for *Coelostomidia zealandica* and *C. wairoensis* differ from previous studies. Towns (2002) reported that the mean number of *C. zealandica* anal tubes per square metre on ngaio on Korapuki Island ranged from 70 to 2200 tubes m^{-2}, whereas no infested ngaio were observed in this study, in either survey plots or in additional searches along the Auckland coastline. As noted above, it is possible that human disturbance has reduced the abundance of ngaio (and other hosts) and/or the abundance of *C. zealandica* in some areas. Alternatively, the heavy ngaio infestations observed on Korupuki Island may be unusual, perhaps arising from the particular pattern of forest recovery on the island that resulted in extensive stands of ngaio available for *C. zealandica* infestation.

Morales (1990) estimated that mean late summer (Feb–Apr) *Coelostomidia wairoensis* densities range from 60 000 to 220 000 per square metre on the terminal 0.4 m of kānuka branches (means estimated from figs 95–97 in Morales (1990)). These estimates are considerably higher than the estimate of 12 400 *C. wairoensis* per square metre from the present study, based on a sample of 25 heavily infested kānuka. The discrepancy may be due to methodological differences. Morales's estimates were based on laboratory counts of live coelostomidiids on kānuka branches and included all feeding stages (instars 1–3). In the present study, densities were estimated by field counts of anal tubes, and this approach is likely to have underestimated the total number of scale insects present. As well, Morales's data suggest there is considerable interannual variation in infestation densities, and this may contribute to the differences between the studies.

Other comparable density estimates come from studies of South Island beech forests. These studies record a wide range of densities for *Ultracoelostoma* species. For example, Beggs et al. (2005) found that mean late summer densities of actively feeding *Ultracoelostoma* spp. on *Nothofagus fusca* ranged from approximately 40 to 700 scale insects per square metre. In contrast, the mean late summer densities recorded for *Ultracoelostoma* spp. on high altitude *Nothofagus solandri* var. *cliffortiodes* ranged from 9 to 17 per square metre (Murphy & Kelly 2003). Both of these studies used the density of honeydew droplets as an indicator of the number of active coelostomidiids present. In the present study, mean honeydew droplet density was 4100 per square metre on heavily infested kānuka (a non-random sample). Estimates based on non-random samples are typically an order of magnitude higher than those based on random samples (Murphy & Kelly 2003). Even so, it appears that *Coelostomidia wairoensis* densities on kānuka are comparable to those recorded for *Ultracoelostoma* species from beech forests.

Conclusions

When distribution and infestation patterns are considered together with the consumer responses, our survey suggests that honeydew is not currently a major component of the ecology of coastal and broadleaved–podocarp forests in the Auckland ER. However, it appears that teatree forests may well be honeydew-influenced as *Coelostomidia wairoensis* infestations are common on kānuka in these forests and *C. wairoensis* honeydew is abundant on heavily infested kānuka trees. This sugar resource could potentially alter the abundance or behaviour of sugar-consumers (Beggs & Wardle 2006) or change soil nutrient cycling (Michalzik et al. 1999; Stadler et al. 1998). Flow-on indirect effects are also possible (Beggs 2001). However, further research is required to quantify the *C. wairoensis* honeydew resource and determine the nature and extent of its impact on the teatree forest community.

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