The influence of honeydew on arthropod community composition in a New Zealand beech forest

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Abstract: The effect of honeydew density on arthropod community structure was investigated in the *Nothofagus* forest of Nelson Lakes National Park, New Zealand. Pitfall trapping revealed no community response to honeydew density, whereas sticky trapping showed the community composition of trunk-dwelling arthropods varied along a honeydew gradient. Mycetophilidae, Staphylinidae, Pteromalidae and Margarodidae were classified as high honeydew biased, while Diapriidae and Platygasteridae were non-honeydew biased. Arthropod distributions within a forest are not uniform, as a result of honeydew patchiness.

Keywords: arthropod community; beech forest; honeydew; *Nothofagus*; pitfall traps; population distribution; scale insect; sticky traps.

Introduction

New Zealand beech (*Nothofagus*) forests are characterised by the honeydew secreted by the scale insect *Ultracoelostoma* spp. (Margarodidae: Homoptera) (Morales, 1991). Honeydew is a sugary exudate and is an important food resource for arthropods (Crozier, 1981; Boyd, 1987; Moller *et al*., 1987; Moller and Tilley, 1989; Harris, 1991; 1992). The density of honeydew varies throughout beech forests due to the response of scale insects to altitude, sunlight, tree age and tree species (Belton, 1978; Crozier, 1978a, b; 1981; Gaze and Clout, 1983; Kelly, 1990). Variation in honeydew density creates a patchy environment within a forest that may impact upon arthropod distributions.

Didham (1993) investigated the role of honeydew in structuring canopy arthropod communities in a mixed forest at Blue Duck Reserve, Kaikoura, New Zealand. He found that arthropod species composition varied between trees infested with scale insects (honeydew trees) and those not infested (non-honeydew trees). Honeydew trees had more Mycetophilidae (Diptera) and Lepidoptera, whereas Blattodea, Thysanoptera and Dolichopodidae (Diptera) were more numerous in non-honeydew trees. Coleoptera and Hymenoptera were equally abundant in both tree types.

This study builds on the work of Didham (1993), who sampled only one honeydew tree that was located on the forest edge. Here, I investigated the role of honeydew in structuring the arthropod community in the beech forest of Nelson Lakes National Park, South Island, New Zealand. The patchiness of the carbohydrate resources provided by the scale insect within beech forest creates an environment with differences in between-patch quality. The differences are expected to have an impact on the composition of arthropod communities within honeydew forest. This study sought to clarify these impacts and determine the relative importance of the honeydew resource to different arthropod taxa.

Methods

Patch location

This study was conducted near Lake Rotoiti (41°49'S 172°51'E) in the Nelson Lakes National Park, New Zealand. The study area was in a mixed beech forest, comprised of silver (*Nothofagus menziesii*), red (*N. fusca*) and mountain (*N. solandri*) beech. The sites have an average annual precipitation range of 1520-2540 mm and average annual temperature of 11-11.5ºC (Bloomfield and Watson 1988).

Three 900-m long transects were marked running parallel to the eastern shore of Lake Rotoiti. The transects were separated by 50 m of altitude. A total of 30 circular patches were placed at 100-m intervals along the transects. Each patch had a 4 m radius and was centred on the closest beech tree with a diameter greater than 14 cm.

Arthropod collection

One pitfall trap was located as near as possible to the base of the central tree in each patch. Each trap was made by cutting the spout off a 1.5 l soft drink bottle and placing it upside down inside the base of the bottle, forming a funnel. Insects were collected at the base of the funnel with a 75 ml sample jar filled three quarters full with water, with the addition of several drops of detergent to break the surface tension. The pitfall traps were left for five nights, from 1 February 1999 to 6 February 1999.

The fauna utilizing tree trunks was sampled with sticky traps. In each patch, one sheet of clear plastic film (an overhead transparency) was stapled 2 m up the trunk of the central tree on its northern aspect. If the central tree was a honeydew tree, the nearest non-honeydew tree with a diameter greater than 14 cm also had a transparency attached. Conversely, if the central tree lacked honeydew, the nearest honeydew tree with diameter greater than 14 cm was chosen for the second transparency. In patches where all trees either had or did not have honeydew, only the central tree had a transparency attached. A paintbrush was used to apply Tanglefoot glue to a 20×20 cm area on each transparency. Sticky traps were 'painted' on 16 February 1999 and collected two days later.

Arthropod identification

Arthropods were transferred from the traps to 70% alcohol for preservation. Sticky trap specimens were removed from the trap by dissolving the Tanglefoot with kerosene. With the exception of mites (Acari), all arthropods in orders with over 20 individuals were identified to family level using keys from Forster (1967), Borror *et al.* (1989), Naumann *et al.* (1991) and Klimaszewski and Watt (1997).

Environmental variables

Thirteen environmental variables were recorded and analysed. These included tree density and vegetation composition reduced to four variables (see statistical analysis section). The distance of each patch to the closest watercourse was estimated to the nearest 50 m, and altitude was recorded to the nearest 10 m. Undergrowth density was scored according to the percentage of the patch covered by vegetation less than 1.5 m high (1 = < 25%, 2 = 26-50%, 3 = 51-75%, 4 = > 75%). An index of trunk surface area (T_t) was calculated for each tree with the equation:

$$T_t = C_t \times 0.25$$

where C_t is the circumference of tree 't' at 2 m height. Thus, T_t represents the surface area of tree 't' that falls within a 25-cm vertical band, related to the height of the sticky trap. Trunk area in the patch (T_p) was estimated by summing T_t.

Honeydew assessment

Counts of scale insect anal filaments were used to calculate an index of honeydew density for all honeydew and non-honeydew trees [after Moller and Tilley (1989)]. The number of filaments on trees less than 14-cm in diameter were counted in a 25-cm band around the trunk centered 2 m high. Honeydew density was determined according to the equation:

$$D_t = X_t / T_t$$

where D_t is the estimated density of honeydew on tree 't' (number of filaments/m^2) and X_t is the number of filaments counted.

Trees over 14 cm in diameter had honeydew density estimated by counting anal filaments in a 10×25-cm quadrat on the north, east, south and west aspects of the tree, all at 2 m height. Honeydew density on these trees was determined by the equation:

$$D_t = [(N_t + E_t + S_t + W_t)/4] / 0.025$$

where D_t is as above, and N_t, E_t, S_t, and W_t are the number of filaments in the north, east, south and west quadrats of tree 't' respectively.

An index of honeydew standing crop on each tree (H_t) was calculated by:

$$H_t = D_t \times T_t$$

As with T_t, H_t represents the standing crop in a 25-cm band centred at 2 m height. Honeydew standing crop in each patch (H_p) was estimated by summing H_t, and was expressed as both a number per m^2 ground area (H_{pg}), and a number per m^2 trunk area (H_{pt}).

Statistical analysis

All data were tested for normality before analysis, and if necessary normalised with log transformations. The pitfall and sticky trap communities were analysed separately. T_t and H_t were omitted from the pitfall analysis.

In the 30 patches, 16 tree species were identified and counted. This data was reduced from 16 independent variables to four with the use of Detrended Correspondence Analysis (DCA), enabling the vegetation community in each patch to be characterised by four numbers (VEG1 to VEG4).

Invertebrate family composition was analysed with Canonical Correspondence Analysis (CCA), using CANOCO version 4 (ter Braak and Smilauer, 1998). Canonical Correspondence Analysis is a multivariate

Table 1. Ordination by CCA on the density of arthropod families collected by pitfall trapping, in relation to 11 environmental variables.

	Axis				
	1	2	3	4	Total inertia
Eigenvalues	0.244	0.206	0.188	0.158	3.411
Family-environment correlation	0.937	0.956	0.931	0.882	
Cumulative percentage variance explained					
Family data	7.2	13.2	18.7	23.3	
Family-environment relation	17.6	32.6	46.1	57.5	
Sum of all unconstrained eigenvalues					3.411
Sum of all canonical eigenvalues					1.384

analysis technique that detects the patterns in community composition that are best explained by linear combinations of known environmental variables (ter Braak, 1986). CANOCO 4 ranks the environmental variables in order of importance by a forward selection procedure somewhat analogous to forward stepwise multiple regression (ter Braak and Verdonschot, 1995). Significance at each step is tested with a Monte-Carlo permutation test using 199 random permutations under the null model of no effect. If the multivariate partial *F*-ratio is within the highest 5% of the *F*-ratios from the randomly generated data sets, the null hypothesis is rejected (Didham *et al*., 1998). To focus on the effect of honeydew, partial CCA was used to remove the effect of significant non-honeydew variables by adding them into the analysis as covariables (Jongman *et al*., 1995). One-way ANOVA was used to test for density responses of specific invertebrate families to significant honeydew indices.

Results

Honeydew assessment

Average honeydew density for all trees (honeydew and non-honeydew) in the patches was 34 anal filaments/m^2 of trunk. For the honeydew trees with sticky traps the average was much higher, at 1238 anal filaments/m^2 of trunk.

Pitfall traps

A total of 510 arthropods were collected, comprising 15 orders, of which the Coleoptera, Hymenoptera, Homoptera and Araneae each had more than 20 individuals and these were identified to family. Canonical Correspondence Analysis revealed that the environmental variables explained little of the variance in family abundance patterns, with eigenvalues for all axes less than 0.25 (Table 1). Only VEG4 explained significant variation in family composition ($\lambda = 0.19$, $F = 1.62$, $P = 0.02$). Neither honeydew/ground area nor honeydew/trunk area were significant predictors of family composition ($\lambda = 0.1$, $F = 1.06$, $P = 0.76$ and $\lambda = 0.11$, $F = 1.01$, $P = 0.61$ respectively).

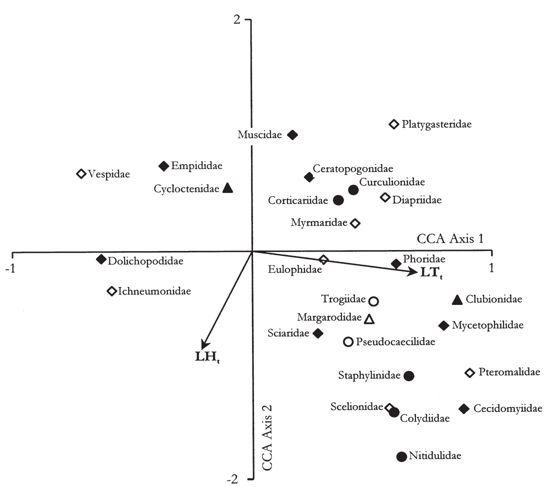

Figure 1. Canonical Correspondence Analysis ordination biplot of family-level density patterns in the arthropod community collected by sticky trapping. The arrows represent the significant environmental gradients superimposed onto the ordination space delineated by CCA Axes 1 and 2. LT_t = index of tree trunk surface area on individual trees, LH_t = honeydew index for individual trees, open diamond = Hymenoptera, filled diamond = Diptera, open circle = Psocoptera, filled circle = Coleoptera, open triangle = Homoptera, filled triangle = Araneae.

Table 2. Ordination by CCA on the density of arthropod families collected by sticky trapping, in relation to 13 environmental variables.

	Axis				
	1	2	3	4	Total inertia
Eigenvalues	0.379	0.256	0.146	0.078	2.499
Family-environment correlation	0.848	0.825	0.813	0.663	
Cumulative percentage variance explained					
Family data	15.2	25.4	31.2	34.3	
Family-environment relation	37.2	62.3	76.6	84.2	
Sum of all unconstrained eigenvalues					2.499
Sum of all canonical eigenvalues					1.019

Sticky traps

A total of 1178 arthropods were collected, comprising 10 orders, six of which had more than 20 individuals (i.e., Araneae, Psocoptera, Coleoptera, Hymenoptera, Diptera and Homoptera) and these were identified to family. Canonical Correspondence Analysis showed that the environmental variables explained a significant portion of the variation in arthropod abundance, in particular the first three axes (Table 2). The first axis separated sites based mostly on trunk surface area, while Axis 2 represented a honeydew gradient and Axis 3 was weakly correlated with tree density. Trunk surface area and trunk standing crop explained significant variation in family composition (Table 3, Fig. 1). These two variables were not significantly correlated (r = -1.31, df = 45, P > 0.1). To determine the sole effect of trunk standing crop a partial CCA was carried out, with trunk surface area as a covariable and trunk standing crop as the impact variable. Trunk standing crop explained 9.1% of the variation in composition at family level ($\lambda = 0.21$, $F = 4.42$, $P = 0.005$).

Analysis of Variance was used to classify the nine most abundant taxa into four groups according to their log density responses to three honeydew categories (high (log $H_t > 3.5$), medium ($0 <$ log $H_t < 3.5$), and absent (log $H_t = 0$)). Four families were high honeydew biased, two were non-honeydew biased, three were honeydew insensitive, and no families were in the medium honeydew biased category (Table 4).

Table 3. Canonical Correspondence Analysis forward selection procedure used to identify the environmental variables significant in determining family composition in the arthropod community collected by sticky trapping.

Marginal effects				Conditional effects				
j	Variable	λ_j	P	j	Variable	λ_a	P	cum (λ_a)
1	LT_t	0.22	0.01	1	LT_t	0.22	0.01	0.22
2	LH_t	0.21	0.01	2	LH_t	0.21	0.01	0.43
3	LH_{pt}	0.13	0.02					
4	LH_{pg}	0.13	0.02					
5	VEG4	0.12	0.04					
6	Altitude (m)	0.09	0.08					
7	Tree density (#/m^2)	0.08	0.11					
8	VEG3	0.07	0.26					
9	VEG2	0.06	0.22					
10	Distance to water (m)	0.04	0.70					
11	LT_p	0.03	0.80					
12	L undergrowth	0.02	0.98					
13	VEG1	0.02	0.96					

L = variable was log transformed prior to analysis, T_t = index of tree trunk surface area on individual trees, T_p = index of trunk area in the patch, H_t = honeydew index for individual trees, H_{pt} = honeydew index for the patch expressed as a number per m^2 trunk area, H_{pg} = honeydew index for the patch expressed as a number per m^2 ground area, λ_j = eigenvalue (fit) with variable j only, λ_a = increase in eigenvalue (additional fit), cum (λ_a) = cumulative total of eigenvalues, P = significance level of effect.

Table 4. Log density responses of invertebrate families collected by sticky trapping to an index of honeydew standing crop (LH_t). Values for the LH_t categories were high ($\log H_t > 3.5$), medium ($0 < \log H_t < 3.5$), and absent ($\log H_t = 0$). Trends in log population density were tested with ANOVA.

Response	Order	Family	n	df	MS(effect)	MS(error)	*F*	*P*	Average Invertebrate Density (#/trap) $LH_t = 0$	LH_t Medium	LH_t High
High honeydew biased											
	Diptera	Mycetophilidae	64	46	0.3521	0.0705	4.993	0.011	4.81	1.43	5.4
	Coleoptera	Staphylinidae	19	46	0.1292	0.0322	4.013	0.025	1.20	0.0	2.58
	Hymenoptera	Pteromalidae	42	46	0.4416	0.0522	8.468	< 0.001	0.10	0.06	0.40
	Homoptera	Margarodidae	29	46	0.1353	0.0336	4.031	0.025	0.12	0.12	0.29
Non-honeydew biased											
	Hymenoptera	Diapriidae	262	46	0.5087	0.1261	4.035	0.025	0.76	0.58	0.43
	Hymenoptera	Platygasteridae	49	46	0.4104	0.0685	5.995	0.005	0.29	0.0	0.02
Honeydew insensitive											
	Diptera	Dolichopodidae	557	46	0.7208	0.3555	2.028	0.144	0.57	0.48	0.94
	Diptera	Phoridae	23	46	0.0069	0.0346	0.200	0.820	0.11	0.12	0.15
	Hymenoptera	Myrmaridae	33	46	0.0794	0.0591	1.342	0.272	0.19	0.0	0.14

Discussion

Scale insect distribution varies greatly with altitude, season, tree species and trees of the same species at different ages, aspects and sites (Crozier, 1978b; 1981; Moller and Tilley, 1989; Kelly, 1990). Kelly (1990) reported densities on black beech that ranged from 4.5-12 anal filaments/m^2, whereas red beech at the same site averaged 118-180 filaments/m^2. At the other extreme are findings from Moller and Tilley (1989). They reported average anal filament densities of 2225/m^2, but their trees were not selected randomly. The site documented in the current study had a low average density (34/m^2). This probably reflects the high proportion of silver beech, upon which scale insect populations are virtually nonexistent (Wardle, 1984).

The index of honeydew standing crop was not an important variable in determining the family composition of the ground-moving arthropod community, indicating honeydew is not an important resource for that community. Honeydew is produced on the trunks and branches of trees, so may not be readily accessible to ground dwelling invertebrates. Some does fall to the ground as splash (Harris *et al.*, 1994), but the amount may be an insignificant food source for litter dwelling arthropods.

In contrast, the tree trunk arthropod fauna was strongly influenced by the standing crop of honeydew on individual trees. This indicates arthropod communities are not uniformly distributed throughout the Nelson Lakes beech forest. Instead, it is possible to view the forest as a system with two communities (non-honeydew and high honeydew) that share several taxa in common (honeydew insensitive).

The surface area of a trunk significantly affected the arthropod community captured on that trunk. This indicates trees of different sizes attract different families of arthropods. This variation may be related to tree physiology. For instance, small *Nothofagus* trunks have smooth bark (Kelly, 1990) and may not offer the same opportunities for species to shelter in bark crevices as large trunks.

This study has probably underestimated the effect of honeydew on the arthropod community. Sticky traps are biased towards the capture of small insects (Basset *et al.*, 1997), meaning an important part of the arthropod community is not represented in this analysis. This is illustrated by the lack of vespulid wasps in the samples, despite the large numbers observed by the author at the time of sampling. As vespulids are the most voracious foragers of honeydew (Moller and Tilley, 1989; Moller *et al.*, 1991; Harris *et al.*, 1994), their absence from the analysis can only diminish the real magnitude of the honeydew effect. Furthermore, arthropods were identified to family level only, which will obscure potentially distinct species-level patterns. It is possible that honeydew insensitive families contain honeydew sensitive species and vice-versa.

These constraints make it difficult to compare the results of this study with the more detailed taxonomy employed by Didham (1993). Despite this, some results from the two studies are comparable. Both studies found the mycophagous Mycetophilidae (Diptera) were more numerous on honeydew trees, where sooty mould (*Capnodium* sp.) provides an abundant food source. Hymenopteran families had both positive and negative responses to honeydew, reflecting Didham's finding that the order Hymenoptera was equally abundant in honeydew and non-honeydew trees. However, Dolichopodidae (Diptera) were honeydew insensitive in this study, whereas Didham found them to be more numerous on non-honeydew trees. Dolichopodids use smooth-barked tree trunks for leks and mating assemblies (Colless and McAlpine, 1991), so it is possible their spatial distribution varies through time. The short sampling period in this study takes a snapshot of the distribution, whereas Didham (1993) trapped over an entire summer, and describes an 'average' distribution through time.

The mechanisms underlying the family responses to honeydew require further study. While honeydew is an abundant food resource, it also supports sooty mould, which provides a complex habitat and further food resources (Didham, 1993). Both the honeydew and sooty mould are likely to be important factors in structuring the arthropod community.

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