Selbyana 20(2): 290–298. 1999.

A Comparison of the Canopy Arthropod Communities of Coniferous and Broad-Leaved Trees in the United Kingdom

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Abstract: The canopy fauna of four coniferous tree species was compared with those of four deciduous broad-leaved species from the UK. Sampling was carried out using pyrethrin knockdown and density and species richness data were standardized to 1 m^2 ground area. Quantitative analyses confirm that the canopies of conifers and broad-leafs support defined but very different communities. For example, mean densities of arthropods were significantly higher for conifers ($P < 0.001$) and when individuals were allocated to feeding guilds, conifers supported proportionately more scavenger/epiphyte feeders whereas broad-leaved trees were dominated by phytophages. The implications of these findings for forest dynamics and herbivore loads are considered. Both groups of trees are dominated by organisms with small body sizes; suggested reasons for this include microclimate and food resources available in the canopy. The species richness of epiphyte feeders and predators was comparable for conifers and broad-leaved trees, however the richness of herbivores was greater on the latter. Woodland specialist species were found in the conifer communities with *Pinus sylvestris* (Scots pine) supporting a particularly rich and dense fauna. The proportion of canopy specialist species, particularly epiphyte feeders, would be expected to increase with maturity of the trees. Although the communities differed from broad-leaved trees it can be concluded that conifers make valuable habitats for arthropods when grown in plantation and can enhance diversity where natural forest is not available.

Key words: Canopy arthropod communities, forest dynamics, conifers, broad-leaved trees

Introduction

The structure and dynamics of tree canopy arthropod communities are less well understood than those of the soil, litter layer and understory. This gap can largely be attributed to the technical difficulties of sampling in a satisfactory and replicable way. However, recent work has demonstrated that on a global scale, the canopy supports a significant proportion of total forest diversity and biomass (Stork 1988, Nadkarni & Parker 1994, Winchester 1997). Canopies therefore need to be studied in a more comprehensive and rigorous manner.

Canopy organisms may be used to test hypotheses about the underlying structure and function of communities. Arthropod assemblages are particularly useful subjects for studies of this type since they are ubiquitous; the assemblages can be diverse; there are numerous individuals in canopies and they are sensitive to environmental change (Kremen et al. 1993). This paper aims to investigate two aspects of community structure using tree canopy arthropods. The first objective is to analyze patterns in abundance and in species richness for several tree species, drawing out similarities and differences. The second is to investigate the constancy of allocation of individuals to guilds on different host plants.

Species Abundance and Richness

Inspection of patterns in the abundance and species richness of organisms can assist in elucidating the role of biotic and abiotic factors in determining community structure. For example, variations in abundance patterns may be indicative of differing resource availability and distribution, or result from environmental and structural variations in the habitat. In their classic study, Kennedy and Southwood (1984) explained differences in arthropod species richness using tree characteristics such as time in the flora, taxonomic relatedness, leaf profile, and area covered. This approach has been exploited usefully by others including Evans (1987) and Moran et al. (1994). Information about abundance and species richness provides useful data to test theories about community assemblage rules and to develop plans for the sustainable management of forests, either plantations or natural managed habitat.

Guild Structure

In 1972 Heatwole and Levins suggested that while communities exhibit species turnover with time, guild structure (sensu Root 1967) might remain constant with respect to species number. Arthropod guild structures have been investigated for some temperate and tropical broad-leaved species (Moran & Southwood 1982, Stork 1987). Although these studies focused on constancy of proportion of species across guilds, Moran and Southwood (1982) also found that when numbers of individuals were considered, the communities were dominated by phytophages (68%). Stork (1987) also found phytophages to be dominant in the tropics although to a lesser degree (26%). Few detailed guild analyses have been carried out for conifer communities but work on old-growth Sitka spruce suggests that assemblages are not dominated by the same guilds (Winchester 1997).

In this study, quantitative comparisons are made between the canopy communities of four coniferous and four broad-leaved trees growing in Southern Britain. In addition, quantitative and qualitative comparisons are made with data from the literature in order to investigate differences in community structure that may be attributable to tree species level variations in the canopy habitat.

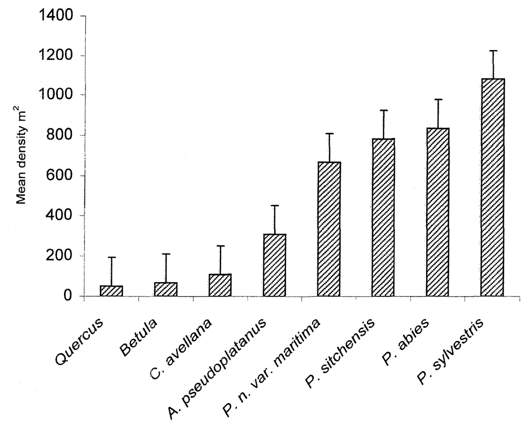


FIGURE 1. Mean densities of arthropods m^{-2} ground area, in the canopies of eight tree species in the UK. (Backtransformed means, + standard error)

MATERIALS AND METHODS

Invertebrate samples were collected from four coniferous species: Scots pine (*Pinus sylvestris* L.), Corsican pine (*Pinus nigra* var. *maritima* Mel.), Norway spruce [*Picea abies* (L.) Karsten] and Sitka spruce [*Picea sitchensis* (Bong.) Carriere]. Trees were approximately 25 years of age and 12–15 m in height. The arthropods were collected at four six-week intervals from June to October 1987. Three independent random samples were taken for the four tree species on each of the sampling occasions. Invertebrate samples were also collected from four broad-leaved tree species growing in mixed woodland; oak (*Quercus* sp.), sycamore (*Acer pseudoplatanus* L.), birch (*Betula* sp.), and hazel (*Corylus avellana* L.). Samples were collected at four six-week intervals from June to October 1994, with five random independent replicates being taken on each occasion.

Invertebrates were collected from the tree canopies using pyrethrin knockdown. The knockdown agent used was Pyrethrin 2/16 (Roussel UCLAF) which consists of a mixture of natural pyrethrins synergized with piperonyl butoxide and delivered to the canopy in a kerosene base. The tree canopies were sprayed using a mist-blower (Hurricane Major—Cooper Pegler), targeting the pyrethrin to a localized area of the canopy. Invertebrates falling from the canopy were collected in a 1 m^2 sheet located directly below the spraying area, from which they were removed and stored in 70% alcohol for identification. The figures shown in this paper therefore refer to arthropod densities and species richness m^{-2} ground area. All spraying was carried out under dry, calm air conditions.

DATA ANALYSIS

The data were analyzed using a general factorial analysis of variance (2-way), with unique sums of squares, except where data required non-parametric analyses (usually due to some cells having no variance, i.e., each count was identical) when the Kruskal-Wallis test was used. Analysis was carried out using SPSS for windows 6.0. Significant differences between means were determined using the Newman-Keuls test. Data for Anova were transformed using log(x + 1) to correct for heterogeneity of variance. Unless otherwise stated, figures for each tree species represent the mean for the whole sampling period, June to October.

The guilds in this study were structured after Root (1967, 1973), Moran and Southwood (1982), and Stork (1987), although insect and arachnid predators are placed in the same category and parasitoids are regarded as specialist predators. The scavenger guild is composed of detritivores and epiphyte feeders.

RESULTS

Abundance Patterns in UK Trees

When the mean numbers of arthropods m^{-2} ground area were compared the eight tree species differed in the densities supported (FIGURE 1). Each of the conifers yielded significantly higher densities of arthropods than any of the four broad-leaved species ($F_{7,96} = 56.13$, $P <$

TABLE 1. Mean arthropod densities per m^2 ground area, collected from the canopies of eight tree species in Southern Britain using pyrethrin knockdown. (Means are backtransformed.) Broad-leaved trees were growing in mixed woodland and coniferous trees in plantation.

	Acarina Mean ± SE			Collembola Mean ± SE			Psocoptera Mean ± SE			Hemiptera Mean ± SE		
	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower
Quercus sp.	2.02	3.46	0.66	1.78	2.44	1.25	8.17	10.17	6.53	4.62	5.57	3.8
Betula sp.	2.12	3.58	0.74	4.56	5.89	3.49	9.62	11.93	7.72	11.45	13.57	9.64
Corylus avellana	2.55	4.32	1.91	11.75	14.8	9.29	7.13	8.91	5.68	19.64	23.15	16.63
Acer pseudoplatanus	2.23	2.72	0.83	44.34	55.18	35.59	11.82	14.62	9.53	95.31	111.72	81.29
Pinus nigra var. *maritima*	203.69	248.3	167.06	192.99	239.37	155.56	12.54	15.49	10.12	59.08	69.32	50.34
Pinus sylvestris	253.69	308.58	207.69	244.49	303.18	197.12	16.81	20.69	13.62	71.81	84.21	61.21
Picea abies	199.07	242.68	163.27	238.82	296.15	192.55	39.98	48.92	32.65	22.95	27.03	19.46
Picea sitchensis	535.32	652.21	439.34	322.35	399.65	259.96	12.67	15.65	10.22	19.64	23.16	16.64

0.001). Sycamore supported the greatest densities among the broad-leafs ($P < 0.001$), with hazel yielding significantly higher densities ($P < 0.001$) than oak and birch, which did not differ.

The densities of individual orders of insects and arachnids did not always follow the same pattern as the overall means (TABLE 1). However, there were similarities within feeding guilds.

Scavengers

The most densely occurring groups on the coniferous trees were the Acarina and the Collembola (TABLE 1). All conifers clearly supported significantly more of these two orders than did the broad-leaved trees ($F_{7,96} = 163.97$, $P < 0.001$ and $F_{7,96} = 81.25$, $P < 0.001$). The Psocoptera were significantly more dense in the canopy of *Picea abies* than in any other tree ($F_{7,96} = 5.86$, $P < 0.001$) (TABLE 1). This agrees with other work on *P. abies* (Ozanne et al. 1997) which shows these insects to be numerically dominant.

Herbivores

The distribution of herbivores differed markedly from that of epiphyte feeders. The Hemiptera were found in high densities on *Acer pseudoplatanus,* significantly higher than all other trees except *Pinus nigra* var. *maritima* and *Picea sitchensis* ($F_{7,96} = 43.07$, $P < 0.001$) (TABLE 1). The mean densities of Lepidoptera were very low in the samples from broad-leaved trees, (<1 m^{-2}). The densities were also low for the conifers, *Picea abies* 4.83 m^{-2}, *Picea sitchensis* 4.5 m^{-2}, *Pinus nigra* var. *maritima* 2.17 m^{-2}, and *Pinus sylvestris* 1.74 m^{-2}.

Other groups

There were less marked differences in the mean densities of Coleoptera, although the order was more prevalent in the broad-leaved trees ($F_{7,96} = 3.56$, $P < 0.002$) and the Diptera were at significantly lower densities on *Quercus* sp., *Betula* sp. and *Corylus avellana* ($F_{7,96} = 13.27$, $P < 0.001$) (TABLE 1).

Predators

Specialist predators (parasitoids) such as the Hymenoptera were less abundant in the canopies

TABLE 1. Extended.

Coleoptera Mean ± SE		Diptera Mean ± SE		Hymenoptera Mean ± SE		Araneae Mean ± SE	
	9.42		4.53		6.94		3.07
7.55		3.58		5.64		2.52	
	6.02		2.79		4.56		2.04
	8.65		3.75		4.09		3.56
6.91		2.94		3.26		2.94	
	5.5		2.26		2.56		2.41
	10.08		6.66		5.98		9.44
8.09		5.35		4.84		8.03	
	6.47		4.26		3.88		6.8
	9.99		18.62		12.05		16.38
8.01		15.25		9.92		14.03	
	6.4		12.47		8.13		11.99
	2.95		24.74		10.73		19.27
2.24		20.33		8.82		16.52	
	1.66		16.67		7.21		14.15
	4.81		15.88		11.03		21.95
3.77		12.99		9.07		18.84	
	2.92		10.59		7.42		16.15
	7.70		15.85		10.23		37.87
6.13		12.96		8.39		32.6	
	4.85		10.57		6.86		28.05
	4.39		17.74		13.78		17.76
3.42		14.53		11.37		15.21	
	2.63		11.87		9.35		13.02

of oak, birch, and hazel than in the other tree species ($F_{7,96} = 4.62$, $P < 0.001$). The densities of spiders were greatest on *Picea abies* ($F_{7,96} = 30.75$, $P < 0.001$) (TABLE 1).

Species Richness

Species richness can be measured by the number of species associated with a tree and the number of species supported per unit area.

According to current species lists *Quercus* spp. and *Betula* spp. have the greatest number of associated arthropod species (TABLE 2). *Pinus sylvestris* has the greatest number of species on the current species list for conifers in the UK while the spruces have fewer, although they are accruing species as their area expands.

TABLE 2. Number of species of phytophagous insects and mites associated with 9 tree species in the UK. (Data are taken from Welch 1986 and Southwood et al. 1982).

Tree	Number of species
Oak	334
Scots pine	263
Norway spruce	178
Larch	100
Beech	98
Sitka spruce	90
Ash	43
Sweet chestnut	11

Data for the number of species per unit ground area (TABLE 3) show that for herbivore-dominated orders, (Heteroptera and Homoptera) species richness was greater on broad-leaved trees. However, for orders of insects such as epiphyte feeders, and predators the richness on coniferous and broad-leaved species was comparable. Some of these arthropods are known to be woodland specialists, e.g., spiders in the genus *Achaearanea.*

Comparative Guild Structure for Densities of Individuals

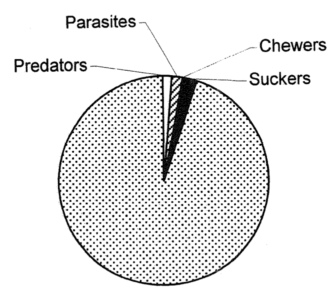
The data for conifers show that, with the exception of Sitka Spruce in May and Norway Spruce in June, the communities are dominated by the scavenger guild. For example, FIGURE 2 shows the guild structure *Pinus sylvestris* in June. The two exceptions to this pattern oc-

TABLE 3. Species richness of five canopy arthropod orders, representing different feeding guilds, 15 m^{-2} ground area. (Standardized to 15m^2 to accord with data from Southwood et al. 1982). (Data for conifers from Ozanne, 1996; data for broad-leaved trees from Southwood et al. 1982).

	Norway spruce	Sitka spruce	Scots pine	Corsican pine	Oak	Birch	Salix alba	Salix cinerea
Psocoptera	9	10	13	9	13	10	6	8
Homoptera	8	9	11	8	25	22	12	15
Heteroptera	2	1	6	1	25	23	12	15
Coleoptera	13	18	11	19	53	30	8	15
Araneae	19	14	24	9	25	23	8	19

curred during outbreaks of the Green Spruce aphid (*Elatobium abietinum*). Guild proportions do vary with month, the most variable guilds being the suckers, chewers, and predators. Suckers are at peak densities on the spruces early in the year and show later peaks on the pines. The

Pinus sylvestris



Quercus sp.

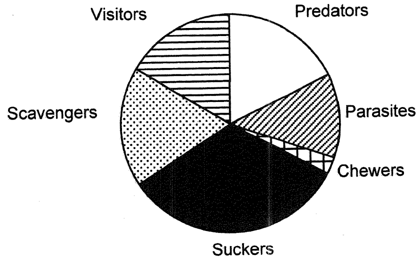


FIGURE 2. Mean densities m^{-2} for individual arthropods, allocated to feeding guilds for one broad-leaved tree, *Quercus* sp. and one coniferous tree *Pinus sylvestris*. Data shown are for the month of June.

proportion of the communities made up of scavengers regularly exceeds 50%, whereas in contrast, the proportion of the communities made up by specialist predators or parasites is remarkably low (0–0.7%). Relatively low levels of parasitism are confirmed by encounters with very few obviously parasitized individuals during identification.

FIGURE 2 also shows the guild structure for *Quercus* sp. in June and demonstrates that the pattern differs from *Pinus sylvestris.* On broad-leaved trees the proportion of the fauna in the phytophage guilds again varied with tree species and across the season. Peak densities of suckers occurred in June for all broad-leaved trees. Epiphyte feeders and scavengers contribute significantly to the fauna at some times of the year for each tree species and the proportions of parasitoids and predators are much higher than on coniferous trees.

DISCUSSION

In the last ten years several studies have investigated the arthropod communities of temperate and tropical trees in a quantitative manner (Stork et al. 1997). However, it is only possible to compare the data from a few of these studies rigorously, because the methodologies are not standardized.

Quantitative analyses confirm that the canopies of different tree species support defined, but very different communities. The figures for the UK conifers agree with those found on other species growing in plantations in temperate regions such as Japan (Kikuzawa & Shidei 1967, Hijii 1983, Hijii 1989). The densities on the UK broad-leaved trees also agree broadly with other studies, although considerable variation can be found for genera such as oak and birch (Watanabe 1997). More detailed comparisons can be made for the communities on broad-leaved trees with data collected using the same methodology in coppiced woodland (Hill et al. 1990). Comparison suggests that mean arthropod densities on hazel and standard birch from mixed wood-

TABLE 4. Mean densities of canopy arthropods m^{-2} ground area for broad-leaved trees in the United Kingdom (UK) and South Africa (SA) (Data taken from Southwood et al. 1982).

Tree genus/ species	Density m^{-2}	Density m^{-2}
	UK	SA
Betula	1290.3 (aphid outbreak)	57.7
Buddleia	186.2	85.5
Quercus	591.3	41.4
Robinia	42.3	120.4
Salix alba	83.5	—
Salix cinerea	139.6	—
Salix carpensis	—	30.7

land tend to be lower and more variable than densities found on oak understory hazel coppice and birch coppice. A further comparison can be made with trees in tropical forest. In primary forest in Borneo arthropod densities are similar to those on broad-leaved trees in the UK: *Shorea johorensis*: 138, *Shorea macrophylla*: 104, *Pentaspadon motleyi*: 109, *Castanopsis*: 178 (Stork 1987). In secondary forest dominated by *Macaranga* spp. mean densities of arthropods were found to be 404 m^{-2} and in *Acacia mangium* plantations 119 m^{-2} (Chey 1994).

The study demonstrates that densities of arthropods m^{-2} ground area are much higher for coniferous trees than for broad-leaved trees. When compared with data from Southwood et al. 1982 (TABLE 4) it can be seen that, with the exception of birch in the UK on which there was an aphid outbreak, the density of arthropods only on oak approaches those found on conifers. Densities are also higher on conifers than on trees in the tropics. This difference can be attributed to the higher leaf area index (LAI) (Tadaki 1966, Ozanne 1996) and to the non-deciduous nature of conifer foliage (Watanabe 1997). These factors lead to more complex canopy architecture and to greater within-canopy microclimate stability, both of which enable the habitat to support a greater number of arthropods (Lawton 1986, Ozanne et al. 1997). Microclimate stability is enhanced further under plantation conditions where trees are planted closely together and gaps are minimized (I. Palmer unpubl. data).

In all temperate tree arthropod communities that have been studied there is a trend towards a larger number of individuals and species with small body size: for individuals this is seen to be at the extreme in plantation conifers. It has been argued that this pattern could result from the greater availability of energy to smaller organisms (Griffiths 1992) and indeed in conifers there is a plentiful food supply for small epiphyte feeders (mean body size <2.5 mm). However, Blackburn et al. (1993), showed that trends in abundance-body size relationships can be predicted by the log-normal distribution and may therefore be independent of energetics. If not wholly explained by availability of food resources, the exaggerated dominance of small organisms in conifers could be ascribed to a reduction in mortality caused by abiotic conditions for small-bodied animals like Collembola. These animals have large surface area to volume ratios and are particularly prone to water loss by convective desiccation, a process that will be reduced in the stable, more humid microclimate of conifer canopies.

Species Richness

Species lists are more complete for well-studied plants and the figures usually given are only for those animals that feed directly on the tree (e.g., phytophagous insects and mites). Figures in TABLE 2 show that in the UK, oak supports the greatest number of invertebrate species, and that the species richness of birch is also high. Although plantation conifers are often supposed to support communities with relatively low species richness the data show no clear separation between deciduous broad-leaved trees and conifers. However, since individual woodlands will only support the proportion of the total species list that is locally available, such lists may not be useful when making decisions about the conservation value of particular woodland types. Data from the woodlands studied here, which lie in southern Britain, show that for insect groups that are entirely or mainly herbivorous, (e.g., Heteroptera and Coleoptera) the number of species supported by broad-leafs is generally higher per unit area. However, for other orders of invertebrates, such as the Psocoptera which are epiphyte feeders, browsing on lichen and algae on the surface of trees and for carnivores such as spiders, the species richness on conifers is directly comparable to broad-leaved trees.

A third approach to the species content of communities is an evaluation of the particular species present in an individual woodland. In the UK, forest area has been expanded by planting mainly non-native conifers, the value of such plantations for biodiversity is a very significant issue. Conifers do not support broad-leaf specialists unless they switch diet or expand their host range. Such changes do occur and Fraser and Lawton (1994) have shown that around 2% of British angiosperm-feeding moths (about 50 species) have been recorded feeding on conifers introduced to Britain. However, conifers do support invertebrates that are woodland specialists.

For example, spiders in the genus *Achaearanea* are equally abundant in broad-leaved and coniferous woodland. Work carried out in Norway spruce shows that 6 to 8 woodland specialist spider species can be found m^{-2} ground area (Ozanne et al. 1997). Woodland specialists feature highly among the species, which are threatened by the impacts of habitat reduction and fragmentation. This study suggests that conifer plantations can provide valuable habitat for these organisms where natural forest is not available.

Guild Structure

The data show that in mid-rotation plantation conifers, canopy arthropod assemblages are dominated by orders with high proportions of scavengers and epiphyte feeders: Acarina, Collembola, and Psocoptera. (The Acarina have a variety of feeding strategies but samples both in plantations and old-growth forest are dominated by fungivorous and saprophagous Oribatid mites (Watanabe 1997, Winchester 1997)). Conifer canopies support higher densities of non-vascular epiphytes such as mosses, lichens, algae, and fungi than deciduous trees, therefore these food resources are abundant and enable trees to support arthropod population densities of up to 390 per m^2 ground area (Collembola on Corsican Pine). In addition, these epiphytes modify the microenvironment allowing microarthropods to exploit it more successfully (Prinzing 1997).

It is possible to compare the communities of plantation-grown conifers in the UK, such as Sitka spruce, with old-growth forest of the same species in the Carmanah Valley, British Colombia, Canada. In these forests, canopy arthropod communities are dominated by the same groups, Diptera, Acarina, and Collembola (Winchester 1997). Key features in the canopy of the old-growth trees are the deep moss mats that support a distinct arboreal fauna (Behan-Pelletier & Winchester 1998). Analysis of collembolan samples from the canopies of Scots pine in North Yorkshire and of Sitka spruce in Kielder forest (I. Palmer unpubl. data), indicate that in UK plantations the dominant species are not arboreal specialists, e.g., *Entomobrya nivalis.* Although *E. nivalis* is found in a range of woodland locations such as tree trunks and terrestrial leaf litter it has been shown to make very specific use of within tree microhabitats in a flexibly responsive manner (Prinzing 1997). It would be expected therefore that as the range and predictability of such microhabitats increases with forest age, e.g., with the development of suspended soils and a more structurally complex epiphyte community, that the associated arthropod communities would become more species rich and develop a specialist component. This proposition remains to be tested in a systematic manner.

In contrast to conifers, Hemiptera frequently dominate the canopy fauna of deciduous broad-leaved trees. Sap feeders such as the Aphididae and Cicadellidae are particularly common in temperate broad-leaved canopies and are often intimately associated with their host species rather than with epiphytes. Fewer species and individuals are found on conifers in the UK. When the data for August in the current study were compared with the Moran and Southwood data (1982), (July/August for Britain and January/February in South Africa), the proportion of chewers and suckers was always lower for the conifers. This suggests that under non-outbreak conditions conifers may be subject to lower herbivore loads than broad-leaved trees.

Differences in guild structure between conifers and broad-leafs suggest that factors underlying community structure on conifers may have a strong abiotic component, whereas on broad-leaved trees biotic factors may be more significant. This is supported by the apparently lower proportions of natural enemies—predators and parasitoids, in the conifer communities. It should be possible to explore this hypothesis further when species level data are available for all orders of arthropods.

Conclusions

The evidence from studies of canopy arthropods shows that conifers support large communities with some species-rich feeding guilds. The communities are both complex in structure and dynamics, and contain woodland specialists. In comparison with temperate broad-leaved trees, the communities on conifers differ in the dominant invertebrate groups and in the specialist herbivores, which they support. However, generalists and specialists occur in high densities.

There are marked differences in the dominant guilds (scavengers/epiphyte feeders and herbivores for conifers and broad-leaved trees respectively) which may result in differences in canopy dynamics which need further exploration. Palacios-Vargas et al. (1998) note that the presence of high densities of scavengers and epiphyte feeders in arboreal habitats should impact canopy nutrient and energy cycling.

To further elucidate the factors that determine community structure and function, we also need to explore the faunas of a greater range of coniferous and deciduous trees in plantation and natural managed forest in temperate regions and the tropics.

Acknowledgments

Funding for the sampling was provided by the Forestry Commission, English Nature and Roehampton Institute London. Thanks to Martin Speight and Hugh Evans for their advice, to Clive Hambler and J.D. Lattin for identifying the Araneae and Heteroptera respectively and to Cath Cotton and Neville Winchester for comments on the manuscript. Thanks also to Pat Morris. Field work assistance was provided by Paul Embden, Imogen Palmer, and Kate Jones. Assistance in finding suitable sites came from the Forestry Commission, Surrey Wildlife Trust, George Blaker, and Andrew Cleave.

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