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Age and distance effects on the canopy arthropod composition of old-growth and 100-year-old *Eucalyptus obliqua* trees

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Abstract

Despite the anthropogenically-induced changes to forest tree demographics, few studies have examined the differences in arthropod species composition between the crowns of trees of different ages. We tested for differences in the taxonomic composition of the canopy arthropod faunas of 100 y.o. and old-growth trees, using eight pairs of trees in an *Eucalyptus obliqua* tall open-forest with a rainforest understorey in the Warra Long Term Ecological Research Site in southern Tasmania and compared these differences to those related to geographic distances. Sticky traps, hanging flight-intercept traps and bark funnel traps were used to sample the canopy arthropods in different placement situations. There were no significant differences between 100 y.o. and old-growth trees at the tree level, but several at the trap and placement levels. Ordination analyses and correlation analyses indicated that high inter-pair variability related to the geographic distance between trees was partially masking tree age effects. The age of *E. obliqua* does influence canopy arthropod species composition, but this effect was weaker than the geographic effect that was evident in a relatively uniform forest with a maximum distance between trees of only 324 m. This implied high beta diversity in the forest type has implications for the planning of conservation reserves. Further work is needed to see if age effects are stronger in forests of the ages created by silvicultural treatment.

Keywords: Canopy arthropods; *Eucalyptus obliqua*; Forest entomology; Geographic distance; Tree age; Tasmania; Invertebrate trapping

1. Introduction

Arthropod biodiversity reaches its greatest levels in forest ecosystems (Erwin, 1995), and Australian *Eucalyptus* forests harbour a globally significant number of species (Majer et al., 1994). Harvesting and replanting alters the structure and demographics of native *Eucalyptus* forests (Lindenmayer et al., 2000). In Tasmania, clearfelled wet eucalypt forests are replanted for potential future harvest on a rotation of 80–90 years. This will result in a reduction in the numbers of old-growth (or veteran) trees, those 110 years or older (Franklin et al., 2002; Lindenmayer et al., 1997). While there are some data on changes in canopy arthropod biodiversity related to the impact of harvesting (Schowalter, 1995; Winchester and Ring, 1996; Chey et al., 1998; Floren and Linsenmair, 2001), and host plant age (Banerjee, 1981; Abbott et al., 1992; Basset, 2001), very little is known about the arthropod biodiversity of old-growth *Eucalyptus* trees in relation to younger trees (Majer et al., 1997). For *Eucalyptus*, the only published study on age-related changes in arthropod communities compares juvenile and sapling *Eucalyptus marginata* (Abbott et al., 1992). No previous research has investigated the differences in arthropod communities between the canopies of mature and old-growth *Eucalyptus* trees.

Previous researchers have found distinctions in the faunal communities between forests, trees, or foliage of different ages. Schowalter (1995) distinguishes a characteristic old-growth forest community on the foliage of western American coniferous forests. In Scandinavian boreal forests, Martikainen et al. (2000) and Sippola and Kallio (1995) found a distinct saproxylic beetle community in older forests when compared to younger managed forests. Waltz and Whitham (1997) found the herbivore arthropod communities within *Populus* crowns to be different between mature and juvenile branches.

Geographically related differences in the arthropod taxon composition of individual trees of the same species and age can occur over relatively short distances. For example, Richardson et al. (1999) showed that differences between the arthropods on individuals of *Melaleuca* occurred systematically over

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0–20 km. Burgman and Williams (1995) found spatial patterning in the foliage arthropod faunas of *E. marginata* trees that became evident at distances of greater than 20 km.

The degrees to which tree age and distance between trees influence arthropod taxon composition in canopies is highly relevant to forest conservation planning, yet there are few data on the subject. The present study uses paired 100-year-old (''100 y.o.'') and old-growth (>350 years, ''old'') trees of *Eucalyptus obliqua* L'Herit. trees. These pairs were distributed over 4 km^2 of tall open-forest with a closed rainforest understorey, at the Warra Long Term Research Site in southern Tasmania, Australia. This design enables the testing of the relative and singular roles of tree age and geographic proximity in influencing canopy arthropod species composition.

2. Methods

2.1. Study area

The study area is on a steep, south-facing slope, between 100 and 300 m above sea level, composed of Jurassic dolerite colluvium overlaying and intermixed with lime-rich Permian sediments. Precipitation approximates 1275 mm per annum with a winter maximum, but no month has an average less than 50 mm. The mean temperature of the warmest month, February is 13.3 °C, and of the coldest, August, is 5.78 °C. The tallest stratum is composed solely of *E. obliqua* trees up to 80 m tall. These have two distinct size classes, which are closely intermixed. The smaller trees date from regeneration after fires between 1898 and 1906 (Hickey et al., 1998). These 100 y.o. trees have crowns of healthy original branches. The old-growth trees are of indeterminable age, but are estimated to be between 350 and 450 years (Hickey et al., 1998). Some of the old trees have a secondary crown of epicormic branches triggered by the fire that enabled the establishment of the younger cohort, while others have a senescing primary crown of original branches (Jacobs, 1955). Beneath the eucalypts is a floristically distinct temperate rainforest canopy 10–30 m tall, dominated by *Atherosperma moschatum* Labill. and *Nothofagus cunninghamii* (Hook.) Oersted.

2.2. Tree pair selection

Eight pairs of *E. obliqua* trees were selected for sampling using the criteria of accessibility and safety for direct rope access into the crown (Dial and Tobin, 1994). Trees in a pair consisted of an old-growth tree and a 100 y.o. tree, and were no more than 50 m apart. All pairs were within a 4 km^2 region. The old-growth trees were selected first, care being taken not to select highly decayed trees that were obviously dangerous for climbers.

2.3. Sampling methods

The canopy arthropod biodiversity of the 16 study *E. obliqua* trees was sampled using three types of trap. Mobile arthropods on the exterior of the tree were targeted. Fourteen trap placements were set within the crown of each tree: two sticky traps, six funnel traps, and six hanging flight-intercept bottles.

The trap design criteria were: broad collection of taxa, low cost, durability in the conditions of the treetops, and portability. Sessile arthropods, and arthropods living within the tree, were poorly sampled by these traps. One sticky trap, composed of a compact disk case coated with Tanglefoot® glue (125 mm × 140 mm), was placed in each of the upper and lower crown of each tree. Funnel traps, composed of the neck of a 1 l soda bottle and a collecting bottle, were nailed to: the upper trunk, the lower trunk, an upper crown dead branch, a lower crown dead branch, an upper crown live branch, and a lower crown live branch. Two 10 mm × 10 mm × 1 m strips of closed cell foam served as drift fences for each funnel trap. For each of the hang traps, an upper and lower bottle collected arthropods intercepted by a plastic panel assembly (200 mm × 120 mm). One hang trap was suspended in each of the lower, middle and upper canopy of each tree.

Traps were active for approximately 60 days between January and April 2004, and collected only once. The upper crown trapping region was approximately 40–45 m high in the 100 y.o. trees, and 55–60 m in the old trees. For the lower crown traps, the region was 20–25 m in the 100 y.o. trees, and 25–30 m in the old trees.

2.4. Arthropod processing

Adult arthropods were identified to distinguishable morphospecies or Recognizable Taxonomic Units (hereafter ''RTU'') and assigned as best as possible to a taxonomic group (Oliver and Beattie, 1996; Pik et al., 1999; Baldi, 2003; Basset et al., 2000). Voucher holotype specimens for each RTU were photographed to aid in identification and archived. Araneae (spiders), Acarina (mites), and Hymenoptera-Formicidae (ants) were counted, but not sorted to morphospecies. Coleoptera (beetles) were pinned and identified, when possible, to named species in the Tasmanian Forest Insect Collection (TFIC), Forestry Tasmania, Hobart, Australia. Araneae were lodged at the Queen Victoria Museum (Launceston, Australia) and Diptera (flies) at the Australian Museum (Sydney, Australia). All other voucher specimens, photo catalogues, and computer CD archives of raw and processed data, are lodged at the TFIC. Digital photographs of each RTU holotype are available for viewing online (http://www.geog.utas.edu.au/yoav/pho/voucher/vouchergallery.htm).

2.5. Data analysis

At the tree level, the independent sampling entity was considered to be a single tree. The entire collection from each of eight 100 y.o. trees was compared to that of each of eight old trees. An assumption was made that the loss of traps was random and unbiased across the two age classes. At the trap level, each trap was considered as a sampling unit and the pool of traps was divided into those from 100 y.o. trees, and those from old trees. Because the individual tree was the subject of consideration, this was a pseudo-replicated approach. Trap level analysis was only used for multivariate community analyses in

which the tree may not be the fundamental unit of distinction between faunas. In these analyses, both age and individual tree identifier were treated as distinct factors. At a placement level, pseudo-replication and lumping of trap results was avoided by only comparing traps of the same placement (design and position). The effect of missing traps was minimized by calculating means for the available traps of a type.

For tree level and placement level, each test between age classes was repeated for each of 24 taxonomic and trap type subsets combining four trap combinations (sticky traps only, funnel traps only, hang traps only, and all three pooled) with six taxa combinations (Coleoptera only, Diptera only, Hemiptera only (true bugs), Hymenoptera only (wasps, bees, ants), and Lepidoptera only (moths and butterflies), and all arthropod taxa combined). Null hypotheses were rejected when $P < 0.05$.

Multi Response Permutation Procedures (MRPP, McCune and Grace, 2002) were used to test the null hypothesis of no difference between the age classes on PC-ORD software (McCune and Mefford, 1999). In multivariate MRPP tests, the dependent variables are the abundance of each RTU collected. This was performed at the trap level and the placement level. When missing traps or the absence of a taxon prohibited MRPP testing, results are labelled ''invalid.''

At a tree level, multivariate non-metric multidimensional scaling ordinations (NMS) were generated using Sorenson/Bray-Curtis distance matrices on PC-ORD to display relative community similarities (Clarke and Warwick, 2001). Points representing study trees were plotted in ordination space, with the distances between points proportional to the dissimilarity of their arthropod communities. Different symbols were used to plot each age class. Study pairs were plotted linked by a vector from the 100 y.o. tree to the old tree. When a trap type in a specific tree had one or no surviving traps, the entire tree was excluded from the analysis. This occurred for sticky traps with one old and one 100 y.o. tree, and also for funnel traps with one old and one 100 y.o. tree. The response of each RTU with greater than 20 individuals collected was examined to determine if any taxa showed a significantly higher abundance in one age class by comparing the mean abundance for each RTU with paired *t*-tests at a tree level.

The physical distances between every possible combination of the 16 trees were calculated from the *x*, *y* and *z* geographic co-ordinates of their base. These values were tested for significant correlations against their taxonomic (Sorenson/Bray-Curtis) distances. This was performed for the tree level data set, and taxonomic and trap type subsets.

One way ANOVA was used to test for significant differences in the mean Sorenson/Bray-Curtis distances between four categories of tree pairings, composed from the 120 possible two-tree combinations of 16 study trees. The four categories were:

(1) Between old: taxonomic distances between the 28 possible combinations of eight old trees.
(2) Between 100 y.o.: taxonomic distances between the 28 possible combinations of eight 100 y.o. trees ($n = 28$).
(3) Between pairs: taxonomic distances between the two trees in each of the eight study pairs ($n = 8$).
(4) Other: taxonomic distances for the 56 other possible pairings of trees, i.e. 100 y.o. trees paired with old trees excluding the study pair combinations.

This was done for the tree level data set, and for taxonomic and trap type subsets. Lepidoptera from sticky traps were excluded. The distances for paired trees were also compared with all other distances.

Table 1
Number of traps processed from eight 100 y.o. and eight old-growth *E. obliqua*, organized by trap design and placement

Trap placement		Traps processed		
		Total	100 y.o.	Old
Sticky	Total	25 (of 32)	12 (of 16)	13 (of 16)
Lower crown	Trunk	13	6	7
Upper crown	Trunk	12	6	6
Funnel	Total	70 (of 96)	35 (of 48)	35 (of 48)
Lower crown	Dead branch	11	6	5
Lower crown	Live branch	13	5	8
Lower crown	Trunk	10	6	4
Upper crown	Dead branch	9	5	4
Upper crown	Live branch	13	6	7
Upper crown	Trunk	14	7	7
Hang trap	Total	91 (of 96)	47 (of 48)	44 (of 48)
Lower crown	Lower bottle	16	8	8
Lower crown	Upper bottle	15	8	7
Mid crown	Lower bottle	16	8	8
Mid crown	Upper bottle	14	7	7
Upper crown	Lower bottle	16	8	8
Upper crown	Upper bottle	14	8	6
All placements	Total	186 (of 224)	94 (of 112)	92 (of 112)

3. Results

One hundred and eighty-six of 224 placed traps were retrieved and processed (Table 1). The total number of traps processed for each age class was similar: 94 traps in the 100 y.o. trees and 92 in the old trees.

Six thousand four hundred and ninety arthropods were collected and classified into 312 RTU. The hang traps caught the most individual arthropods (2628), followed by the funnel traps (2724). The sticky traps caught the least number of animals (1240).

Approximately half of all RTU were found only in one age class, and half were found in both age classes (Table 2). Slightly more RTU were found in old trees only than in 100 y.o. trees

Table 2
Number of arthropod Recognizable Taxonomic Units collected in eight 100 y.o. and eight old-growth Tasmanian *Eucalyptus obliqua* crowns at Warra LTER

Trap type	100 y.o. only	Old only	Both	Total
Sticky	27	41	42	110
Funnel	62	36	81	179
Hang	62	79	100	241
All traps	75	82	155	312

Table 3
MRRP *P*-value results at a trap level testing a null hypothesis of no difference in the composition of arthropods collected in the crowns of eight 100 y.o. and eight old-growth Tasmanian *E. obliqua* crowns at Warra LTER

Trap type	Traps compared	# traps 100 y.o.	# traps old	All arthropods	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera
Sticky	All sticky traps pooled	12	13	0.26	0.68	0.39	0.85	0.73	0.50
Funnel	All funnel traps pooled	35	35	0.22	0.39	0.26	0.85	0.32	0.87
	Trunk traps only	13	11	0.29	0.65	0.26	0.96	0.55	0.95
	Live branch traps only	11	15	**<0.01*****	0.30	0.20	0.27	**0.01****	(invalid)
	Dead branch traps only	11	8	0.38	0.12	0.65	0.33	0.66	(invalid)
	Live and dead pooled	22	24	**<0.01*****	0.24	0.08	0.51	**0.01****	(invalid)
Hang	All hang, both bottles	47	44	0.96	0.27	1.00	0.29	0.30	0.35
	Upper bottles only	23	20	0.42	0.72	0.66	0.23	0.45	0.63
	Lower bottles only	24	24	0.16	**0.03***	0.20	0.12	0.06	0.28
All traps pooled	All placements pooled	94	92	0.46	0.35	0.58	1.00	0.42	(invalid)

Significant differences are highlighted in bold.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

only. For both hang traps and sticky traps, more RTU were collected in old trees only than in 100 y.o. trees only. The results for the funnel traps were different. Almost twice as many RTU were found only in funnel traps in 100 y.o. trees than were found only in funnel traps in old trees.

At a trap level, several significant differences in RTU composition were identified with MRPP tests (Table 3). The collection of all funnel traps placed on live branches was significantly different between ages. This trend appeared to be driven by the Hymenoptera, and to a lesser extent, the Diptera. The lower bottles of all hang traps pooled collected a significantly different beetle fauna. No significant differences in composition were detected in the fauna of sticky or funnel traps on the trunks. Analysis of lepidopteran fauna was not always possible due to their relatively low abundances.

At a placement level, three significant differences in composition were detected with MRPP tests (Table 4). The composition of arthropod communities was significantly different for lower live branch funnels, and in the lower bottle of the upper hang trap. The fly composition was significantly different between ages in the lower bottle of the uppermost hang trap.

None of the taxa that had a total abundance of 20 or more were collected only from trees of one age (Table 5). However, many were concentrated in either old or 100 y.o. trees (Table 5). A beetle, *Rodatus* TFIC sp. 01, and a moth, Oecophoridae YDB sp. 7, were significantly more abundant in 100 y.o. trees. Two

Table 4
MRRP *P*-value results at a placement level testing a null hypothesis of no difference in the composition of arthropods collected in the crowns of eight 100 y.o. and eight old-growth Tasmanian *E. obliqua* crowns at Warra LTER

Trap type	Placement	All arthropods	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera
Sticky							
Lower crown	Trunk	0.37	0.89	0.47	0.65	1.00	0.30
Upper crown	Trunk	0.76	0.41	0.67	0.83	0.74	(invalid)
Funnel							
Lower crown	Dead branch	0.63	0.07	0.37	(invalid)	0.36	(invalid)
Lower crown	Live branch	**0.01****	0.75	0.23	0.77	0.11	(invalid)
Lower crown	Trunk	0.09	0.79	0.13	0.93	0.37	0.34
Upper crown	Dead branch	0.19	0.81	(invalid)	(invalid)	0.13	(invalid)
Upper crown	Live branch	0.08	0.58	0.47	(invalid)	0.19	(invalid)
Upper crown	Trunk	0.89	0.62	0.86	0.85	0.44	0.71
Hang trap							
Lower crown	Lower bottle	0.90	0.27	0.89	1.00	0.36	0.17
Lower crown	Upper bottle	0.23	0.24	0.10	0.56	0.70	0.75
Middle crown	Lower bottle	0.52	0.10	0.64	0.25	0.19	0.77
Middle crown	Upper bottle	0.97	0.57	0.93	0.21	0.06	0.79
Upper crown	Lower bottle	**0.03***	0.25	**0.04***	0.66	0.19	0.30
Upper crown	Upper bottle	0.37	0.53	0.10	0.75	0.87	0.41

Significant differences are highlighted in bold. The number of trees contributing to each placement for each age class can be read directly from Table 1.
* $P < 0.05$.
** $P < 0.01$.

Table 5
Total collection and mean abundances per tree compared between 100 y.o. and old-growth *E. obliqua* for taxa with total abundance of 20 or more

Taxon	Ratio old/ 100 y	Total abundances 100 y.o.:old				Abundance per tree: mean (S.D.)		Frequency (trees)	
		All traps	Sticky	Funnel	Hang	100 y.o.:old	*P*	100 y.o.	Old
All arthropods	0.86	3485: 3005	644:596	1596: 1128	1245:1281	435.6 (210.9): 375.6 (165.5)	0.54	8 (of 8)	8 (of 8)
Plecoptera YDB sp. 1 (Plecoptera)	0.06	36:2	0:0	36:2	0:0	6.0 (7.4):1.0 (0.0)	0.10	6	2
Rodatus TFIC sp. 01 (Coleoptera)	0.08	25:2	0:0	25:2	0:0	**3.6** (2.9):1.0 (0.0)	**0.02***	5	2
Sciaridae YDB sp. 11 (Diptera)	0.14	70:10	45:2	1:7	4:1	10.0 (13.9):3.3 (3.2)	0.14	7	3
Acarina	0.18	85:15	4:1	69:9	12:5	12.1 (17.2):3.0 (2.3)	0.16	7	5
Barconida YDB sp. 3 (Hymenoptera)	0.20	20:4	16:2	0:0	4:2	4.0 (3.1):2.0 (1.4)	0.11	6	2
Oecophoridae YDB sp. 7 (Lepidoptera)	0.23	26:6	0:1	12:0	14:5	**3.7** (2.9):2.0 (1.0)	**0.05****	7	3
Sciaridae YDB sp. 09 (Diptera)	0.28	61:17	60:11	1:0	0:6	20.3 (19.7):3.4 (3.3)	0.32	5	5
Blatellidae YDB sp. 3 (Blattodea)	0.32	28:9	0:0	26:4	2:5	2.6 (6.1):2.3 (2.5)	0.27	7	4
Orphanotrophium frigidum (Coleoptera)	0.33	18:6	13:4	2:1	3:1	4.5 (6.4):1.5 (1.0)	0.40	5	4
Cicadellidae YDB sp. 02 (Hemiptera)	0.40	15:6	0:2	15:3	0:1	2.5 (1.6):2.0 (1.7)	0.18	4	3
Diptera YDB sp. 16	0.40	57:23	57:23	0:0	0:0	8.1 (8.3):3.8 (1.7)	0.18	7	6
Phoridae YDB sp. 1 (Diptera)	0.53	19:10	15:9	0:0	4:1	3.8 (5.2):5.0 (5.7)	0.56	5	2
Hymenoptera YDB sp. 05	0.53	30:16	28:11	1:3	1:2	10.0 (13.9):2.7 (2.2)	0.60	5	6
Oecophoridae YDB sp. 2 (Lepidoptera)	0.54	37:20	1:1	30:16	6:3	6.2 (8.0):5.0 (4.5)	0.48	8	4
Cosmopterygidae YDB sp. 1 (Lepidoptera)	0.58	26:15	0:0	0:0	26:15	3.7 (2.8):2.5 (1.9)	0.29	7	6
Flugoridae YDB sp. 1 (Hemiptera)	0.65	31:20	13:15	11:3	7:2	4.4 (4.2):2.9 (2.5)	0.44	5	7
Flatidae YDB sp. 1 (Hemiptera)	0.66	35:23	0:0	34:22	1:1	7.0 (5.8):4.6 (3.8)	0.54	7	5
Aulonothroscus elongatus (Coleoptera)	0.67	155:104	11:20	110:56	34:28	19.4 (16.1):13.0 (14.4)	0.42	7	8
Tipulidae YDB sp. 1 (Diptera)	0.68	56:38	0:0	31:24	25:14	8.0 (6.8):6.3 (5.3)	0.48	3	6
Chrysophtharta bimaculata (Coleoptera)	0.69	13:9	0:1	9:4	4:4	2.6 (1.5):1.1 (0.4)	0.45	5	8
Sciaridae YDB sp. 03 (Diptera)	0.72	630:452	20:14	229:96	381:342	78.8 (58.3):56.5 (45.3)	0.41	8	8
Sciaridae YDB sp. 10 (Diptera)	0.76	87:66	72:55	0:34	7:4	12.4 (9.9):9.4 (4.9)	0.53	7	7
Tipulidae YDB sp. 4 (Diptera)	0.80	40:32	5:0	28:11	7:21	5.7 (4.6):5.3 (5.8)	0.70	6	6
Pompilidae YDB sp. 1 (Hymenoptera)	0.82	22:18	0:5	18:10	4:3	3.1 (2.0):3.6 (2.5)	0.68	4	5
Sciaridae YDB sp. 02 (Diptera)	0.83	132:110	46:21	43:49	43:40	16.5 (12.7):13.8 (8.4)	0.62	8	8
Tipulidae YDB sp. 2 (Diptera)	0.84	19:16	0:1	1:1	18:14	3.2 (1.7):2.7 (0.8)	0.68	5	6
Pentatomidae YDB sp. 3 (Hemiptera)	0.86	57:49	0:0	56:48	1:1	9.5 (7.2):7.0 (6.3)	0.78	4	7
Geometridae YDB sp. 1 (Lepidoptera)	0.86	43:37	0:3	40:27	3:7	10.8 (8.3):5.3 (7.2)	0.84	7	7
Diptera YDB sp. 06	0.90	351:317	103:135	120:53	128:129	43.9 (28.5):39.6 (22.0)	0.74	7	8
Cicadellidae YDB sp. 08 (Hemiptera)	0.96	56:54	0:0	53:51	3:3	8.0 (10.5):9.0 (9.4)	0.96	7	6
Blatellidae YDB sp. 4 (Blattodea)	0.97	38:37	0:1	34:34	4:2	5.4 (5.9):4.6 (5.3)	0.96	6	8
Oecophoridae YDB sp. 1 (Lepidoptera)	1.00	25:25	0:0	0:8	25:17	3.1 (1.7):5.0 (3.3)	1.00	4	5
Phalacridae TFIC sp. 01 (Coleoptera)	1.00	10:10	0:1	0:2	10:7	1.7 (0.8):2.5 (2.4)	1.00	3	4
Araneae	1.05	155:163	2:3	94:83	59:77	19.4 (8.2):20.4 (8.6)	0.82	7	8
Blatellidae YDB sp. 5 (Blattodea)	1.08	26:28	0:0	23:25	3:3	5.2 (2.3):4.0 (3.3)	0.88	3	7
Cicadellidae YDB sp. 06 (Hemiptera)	1.11	19:21	1:0	17:19	1:2	2.7 (2.05):3.0 (2.2)	0.82	5	7
Phoridae YDB sp. 3 (Diptera)	1.20	88:106	9:23	15:7	64:76	12.6 (19.4):13.3 (18.3)	0.81	6	8
Isoptera YDB sp. 1 (Isoptera)	1.23	13:16	2:1	7:6	4:9	1.9 (0.9):2.7 (14.1)	0.60	2	6
Tortricidae YDB sp. 1 (Lepidoptera)	1.35	17:23	0:0	0:0	17:23	2.4 (1.6):4.6 (6.1)	0.70	7	8
Hymenoptera YDB sp. 17	1.36	11:15	11:7	0:2	0:6	5.5 (4.9):3.0 (2.3)	0.73	2	5
Mycetophilidae YDB sp. 7 (Diptera)	1.55	11:17	0:0	0:16	11:1	2.2 (1.6):8.5 (10.6)	0.72	6	5
Formicidae (Hymenoptera)	1.66	88:146	0:21	64:111	24:14	12.6 (9.6):18.3 (16.2)	0.30	4	2
Chalcidoid? YDB sp. 1 (Hymenoptera)	1.73	22:38	12:16	7:18	3:4	3.1 (2.8):5.4 (2.2)	0.18	7	8
Pentatomidae YDB sp. 4 (Hemiptera)	1.76	17:30	0:1	17:25	0:4	2.8 (1.7):5.0 (5.4)	0.42	5	7
Dorhnia simplex (Coleoptera)	1.87	15:28	0:0	13:23	2:5	3.0 (3.1):4.0 (3.8)	0.35	7	6
Anobiidae YDB sp. 01 (Coleoptera)	2.93	14:41	5:10	2:7	7:24	2.3 (2.3):**5.1** (2.6)	**0.01****	7	7
Trogossitidae TFIC sp. 01 (Coleoptera)	3.10	10:31	2:12	4:4	4:15	2.0 (1.7):**4.4** (2.6)	**0.04***	6	8
Eurymelidae YDB sp. 02 (Hemiptera)	3.50	8:28	0:0	3:26	5:2	2.0 (1.4):28.0 (inv)	0.49	6	7
Blatellidae YDB sp. 2 (Blattodea)	3.56	9:32	0:0	9:26	0:6	2.3 (1.3):5.3 (5.4)	0.16	7	1
Mycetophilidae YDB sp. 2 (Diptera)	7.75	4:31	3:28	1:0	0:3	2.0 (1.4):7.8 (12.2)	0.31	7	6

Taxa are ranked by total collection ratio of 100 y.o. to old, i.e. from most relatively common on 100 y.o. trees to most relatively common on old trees. *P*-values are from paired *t*-tests comparing mean abundance per tree. Significant differences are highlighted in bold. The acronym "YDB" refers to a working holotype designated from this research project, and the acronym "TFIC" refers to a working holotype at the Tasmanian Forest Insect Collection, Hobart, Australia.

* $P < 0.05$.

** $P < 0.01$.

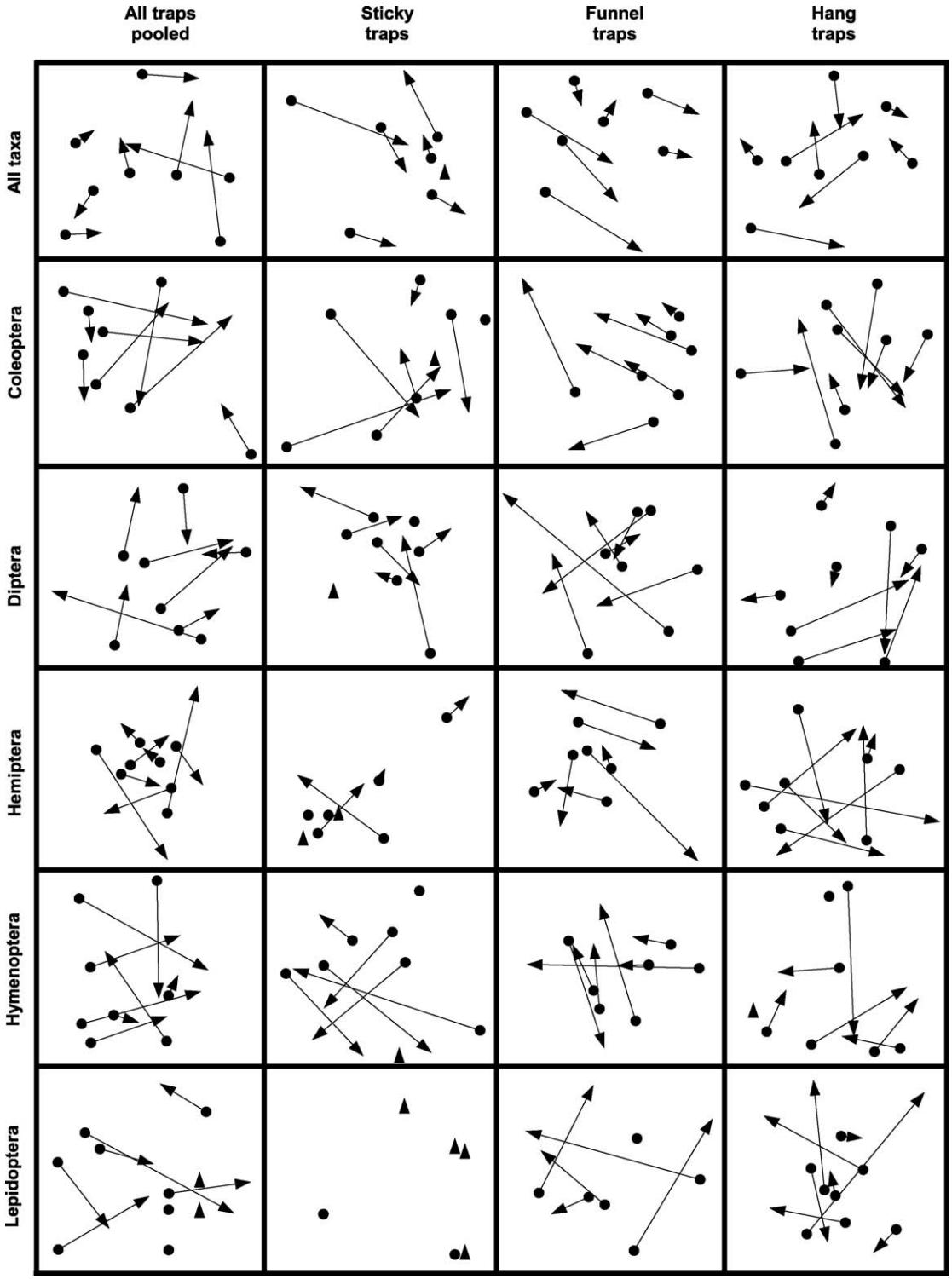

Fig. 1. NMS ordinations of arthropods collected in the crowns of 16 Tasmanian *Eucalyptus obliqua*, for 24 combinations of taxa and trap type: (●) 100 y.o. trees and (▲) old trees. Study pairs are linked. The triangle is rotated to aid in visualization. When missing traps or the absence of a taxon left an old tree without its study pair, the triangle was arbitrarily pointed upwards. Insufficient numbers of Lepidoptera were collected in sticky traps to compare any study pairs.

beetles that were significantly more abundant in old trees were Anobiidae YDB sp. 01 and Trogossitidae TFIC sp. 01.

NMS ordinations illustrated several trends in composition between and within tree pairs (Fig. 1). Linked pairs (forming arrows) pointing in the same direction showed a parallel, analogous change in faunal composition between ages for different pairs. This was exhibited by the total arthropod collection in the funnel and sticky traps, and the Coleoptera in the funnel traps.

Clustered groups of trees from one age class and scattered trees from the other were evident in several of the ordination diagrams, and significant in the ANOVA analysis (Table 6).

Table 6
Mean Sorenson/Bray-Curtis distances for different categories of comparison, showing the results of one way ANOVA and Tukey's multiple comparison test (letters) and the rank order of the row types (in parentheses)

Taxon	Trap	Between old	Between 100 y.o.	Between pairs	Other
All	All	**0.558b (3)**	**0.578b (1)**	**0.512a (4)**	**0.573b (2)**[a,*]
Coleoptera	All	0.611 (3)	0.644 (2)	0.601 (4)	0.679 (1)
Diptera	All	0.412 (1)	0.397 (3)	0.371 (4)	0.399 (2)
Hemiptera	All	0.659 (1)	0.629 (3)	0.587 (4)	0.632 (2)
Hymenoptera	All	0.660 (4)	0.665 (2)	0.662 (3)	0.706 (1)
Lepidoptera	All	**0.622a (1)**	**0.482b (4)**	**0.546ab (3)**	**0.579a (2)**[***]
All	Sticky	0.655 (3)	0.700 (1)	0.648 (4)	0.685 (2)
Coleoptera	Sticky	**0.638a (4)**	**0.826b (1)**	**0.718ab (3)**	**0.730a (2)**[**]
Diptera	Sticky	0.567 (1)	0.519 (4)	0.550 (2)	0.527 (3)
Hemiptera	Sticky	0.638 (2)	0.646 (1)	0.482 (4)	0.614 (3)
Hymenoptera	Sticky	0.806 (3)	0.709 (4)	0.825 (1)	0.819 (2)
All	Funnel	0.687 (2)	0.685 (3)	0.644 (4)	0.693 (1)
Coleoptera	Funnel	**0.773b (2)**	**0.647a (4)**	**0.673ab (3)**	**0.787b (1)**[**]
Diptera	Funnel	0.514 (4)	0.539 (3)	0.599 (1)	0.554 (2)
Hemiptera	Funnel	0.631 (1)	0.533 (4)	0.593 (2)	0.568 (3)
Hymenoptera	Funnel	0.676 (4)	0.679 (3)	0.700 (2)	0.728 (1)
Lepidoptera	Funnel	0.742 (3)	0.638 (4)	0.822 (1)	0.743 (2)
All	Hang	0.617 (1)	0.613 (2)	0.542 (4)	0.607 (3)
Coleoptera	Hang	**0.677a (4)**	**0.787b (1)**	**0.715ab (3)**	**0.750b (2)**[**]
Diptera	Hang	0.489 (1)	0.456 (3)	0.426 (4)	0.472 (2)
Hemiptera	Hang	0.836 (2)	0.829 (3)	0.891 (1)	0.818 (4)
Hymenoptera	Hang	0.859 (3)	0.886 (1)	0.810 (4)	0.879 (2)
Lepidoptera	Hang	**0.704c (1)**	**0.501a (4)**	**0.582abc (3)**	**0.620b (2)**[***]

Significant differences are highlighted in bold. The same letter against values in a row indicates that the values are statistically identical at $P > 0.05$.
[a] Significant difference for comparison of "between pairs" and "other".
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

Lepidoptera in all traps and the hang traps, and Coleoptera in the funnel traps had tighter clustering in the 100 y.o. trees than the old trees. The old trees had the more clustered fauna for Coleoptera in sticky traps and hang traps. Clustering was observed in which each age class tended to its own zone. This was observed for the Hymenoptera in the sticky traps.

The mean of the taxonomic distances between the study pairs old and 100 y.o. trees for all traps and all taxa was significantly less than the mean for all other distances pooled (Table 6). The mean of the distances between old and 100 y.o. trees that were not in pairs (between other) was significantly greater than the mean of the distances between 100 y.o. trees for Lepidoptera in all traps and hang traps, and for Coleoptera in funnel traps (Table 6). The reverse pertained for Coleoptera in sticky traps. The mean of the distances between old and 100 y.o. trees that were not in pairs (between other) was significantly greater than the mean of the distances between old trees for Coleoptera in hang traps. The reverse pertained for Lepidoptera in hang traps (Table 6).

There were weak, but significant, positive relationships between geographic distances and taxonomic distances for all taxa in all traps ($r = 0.240$, $P < 0.01$), Diptera in all traps ($r = 0.248$, $P < 0.01$), all taxa in funnel traps ($r = 0.243$, $P < 0.05$), and Lepidoptera in hang traps ($r = 0.181$, $P < 0.05$).

4. Discussion

Overall, differences in the trapped arthropod faunas of paired old and 100 y.o. trees were weak, with funnel traps on branches and lower canopy hang traps producing all of the few significant differences (Tables 3 and 4), and only 4 out of the 50 most abundant base level taxa being significantly more abundant in older or younger trees (Table 5). Significant values have such a low incidence that they could be interpreted to have occurred by chance. However, their concentration in particular trap types and positions suggests otherwise, as does the nature of the organisms involved.

The fact that the mean of the taxonomic distances between paired trees for all taxa in all traps is significantly less than the mean of all other taxonomic distances between pairs of trees (Table 6) does not support a primary role of tree age in influencing faunal assemblages caught with these particular traps in this particular forest with these particular ages. One hundred year old trees are approaching old-growth status, to be declared formally at 110 years, and the older trees were selected, for safety reasons, on the basis of their lack of extreme decay. Faunal differences may have been more marked if the younger trees had been more developmentally distinct from the old trees. This supposition is weakly supported by the nature and results of the comparisons in the limited previous literature (Abbott et al., 1992; Schowalter, 1995; Martikainen et al.,

2000; Sippola and Kallio, 1995). However, many more comparisons are needed to build up an adequate meta data set. In addition, the trapping methods sampled from the surface and crown airspaces of the trees, both of which are habitats that may be fundamentally similar between trees of different ages. Xylophilic species assemblages may be more distinct between the older and younger trees, as has been suggested by some ongoing work in the same forest on fallen trees of different sizes (Yee, 2005), but these animals, and other arthropods in the tree interior, were not likely to have been adequately sampled by the traps used in the present study.

In three of the data sets in which there was a significant difference in the mean of the taxonomic distances between 100 y.o. trees and the mean of the taxonomic distances between old trees, the older tree mean distances were greater, while the reverse pertained in two comparisons (Table 6). In the only other comparable study, Schowalter (1995) reported a distinct, consistent arthropod community on the foliage of old-growth Oregonian conifers, with trees in younger forests harbouring a subset of the old-growth forest community, but with more variability in composition. His older forest replicates were more similar to each other than the younger forests were to each other. Given the above variability in results, much more work would be desirable in this area.

Geographic distance between trees had a significant positive linear relationship with taxonomic distance between trees in four out of 23 analyses, indicating a stronger role of geographic position than age of tree in influencing faunal species composition. This stronger role is also indicated by the generally higher mean distance values for old to 100 y.o. tree comparisons outside the pairs than between the pairs (17 versus 6, Table 6). The maximum geographic distance between trees was only 324 m, rather than the 20 km plus for which distance effects on arthropod faunas of other Myrtaceae tree species were deduced by Burgman and Williams (1995) and Richardson et al. (1999). However, their analyses were not as finely partitioned as those in the present paper, so it cannot be concluded that this apparent difference is necessarily real. This geographic effect may be linked to unmeasured changes, such as understorey composition (Recher et al., 1996) or site productivity (Yen and Lillywhite, 1990).

In two of the present analyses, both of funnel traps, the most likely type to capture xylophilic species, the geographic effect masked an age effect (Fig. 1), suggesting that environmental variation related to geographic position may effect arthropod species composition in a similar way to environmental variation associated with tree age.

5. Conclusions

A difference in age of *E. obliqua* trees of 100 years compared to c350 years influences arthropod species composition, but geographic position within the stand appears to be a stronger influence.

The fact that geographic variation in arthropod assemblages in the canopies of the same species of tree can occur within a distance of 324 m suggests that this forest type may have relatively high canopy arthropod beta diversity in stands 100 years or older. A high beta diversity suggests that reservation strategies for these forests need to be designed to cover their geographic range, a strategy that may favour many relatively small reserves over a few large reserves, for any proportional reserve target. Given that the prevailing silvicultural treatment of these forests involves an 80–90 years rotation, it is obviously important to make comparisons of the canopy faunas of the 100–350+-year-old trees like those included in the present study with younger trees. Such a study could better determine if age effects, in the age range likely to be created by silvicultural operations, are relevant to conservation planning for canopy invertebrates. Studies of vascular plants (Hickey, 1994) and bryophytes (Turner, 2003) in the same forest type have revealed some strong age effects on species composition in the forests as a whole in the 0–80 years age range, so stronger age effects than those apparent in the present study may also occur with canopy invertebrates.

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