

Tree holes in a mixed broad-leaf–podocarp rain forest, New Zealand

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Abstract: Despite the ecological importance of tree holes as habitat for many species in New Zealand, few studies have quantified the abundance, distribution or structural characteristics of tree holes in native forests. We recorded a total of 364 tree holes in ground-to-canopy surveys on 50 trees of five endemic species in the families Fagaceae and Podocarpaceae within Orikaka Ecological Area, Buller District, New Zealand. Tree holes were not uniformly distributed throughout the forest, with more holes in the three podocarp species *Prumnopitys ferruginea*, *P. taxifolia* and *Dacrycarpus dacrydioides* than in *Nothofagus fusca* or *N. menziesii*. However, *N. fusca* had the largest tree holes of any of the tree species sampled. Tree-hole volume and tree-hole opening both increased with tree size. Tree-hole opening was strongly positively correlated with internal volume, especially for the podocarps. It therefore potentially provides a useful surrogate measure for quantifying the abundance of large tree holes from cost-effective ground surveys. We estimated there might be as many as 771 tree holes per hectare of forest at this site, but fewer of these were thought to be large enough for obligate hole-dwelling vertebrate species. Our findings differ from those of previous researchers in native forests around New Zealand because earlier studies used ground-based surveys to sample the abundance of tree holes suitable for specific fauna, whereas we used climbed inspections where all tree holes were recorded. These differences in tree-hole estimates per hectare could be particularly important for the conservation management of native vertebrate and invertebrate species.

Keywords: *Dacrycarpus*; forest canopy; microhabitats; *Nothofagus*; *Prumnopitys*

Introduction

Tree holes provide important ecological resources for many vertebrate and invertebrate species throughout the world (Kitching 1971, 2001; Greeney 2001; Yanoviak 2001; Gibbons & Lindenmayer 2002; Ranius 2002). In New Zealand, water-filled tree holes support an array of aquatic insect species (Taylor & Ewers 2003; Derraik 2005; Derraik & Heath 2005; T.J. Blakely, unpubl. data), while dry tree holes are known to be important nesting and roosting sites for a wide range of native obligate hole-dwelling bird and bat species (e.g. stitchbird *Notiomystis cincta*, saddleback *Philesturnus carunculatus*, mohua *Mohoua ochrocephala*, yellow-crowned kakariki *Cyanoramphus auriceps*, long-tailed bat *Chalinolobus tuberculatus* and lesser short-tailed bat *Mystacina tuberculata*; Robertson 1985; Elliott et al. 1996; Greene 2003; Sedgely 2003), as well as many exotic bird and mammalian species. However, despite the undoubted importance of tree holes for endangered species, the distribution and frequency of tree holes have remained largely unstudied in the native forests of New Zealand (but see Rasch 1989; Elliot et al. 1996; Sedgely 2001, 2006). A recent study in the Lewis Pass, New Zealand, found that tree holes may be very

abundant in old-growth *Nothofagus* forest (Blakely et al. 2008), but little is known about the abundance of tree holes in mixed broad-leaf–podocarp forests. In particular, no direct comparisons of the spatial distribution of tree holes and their structural characteristics have been made between podocarp and *Nothofagus* species within the same forest.

In New Zealand forest ecosystems, tree holes form when a tree is exposed to physiological or physical stressors including wounding from mechanical-scarring or incomplete branch abscission, stochastic storm events, fungal and invertebrate attack, and increasing tree age (Stewart & Burrows 1994; Peterson 2000). A wide range of factors can influence the development and abundance of tree holes, including individual-tree characteristics, such as diameter, age, species, health and growth habit, as well as site features such as stand basal area, slope, topographic position and rainfall (Bennett et al. 1994; Lindenmayer et al. 2000; Whitford 2002; Fan et al. 2003).

Perhaps most importantly, size and age structure of the forest can have a primary influence on the distribution and abundance of tree holes, with older, larger trees having more tree holes than young trees (Gibbons & Lindenmayer 2002, Blakely et al. 2008). Consequently, deforestation

and logging practices that alter the age structure of forest stands can reduce the abundance of tree holes and their associated wildlife. Reduced availability of tree-hole habitat can result from two interrelated processes: first, the direct loss of hole-bearing trees due to removal for timber and, second, the limitation of recruitment of trees into hole-bearing cohorts. Tree harvesting and selective logging generally target large trees (Wardle 1984) and therefore reduce the availability of roosting/nesting sites for obligate hole-dwelling species (Mackowski 1984; Lindenmayer et al. 1991). Ball et al. (1999) developed a simulation model in a monospecific Australian eucalypt forest showing that when the harvest rotation is 100 years or less, a long-term supply of hole-bearing trees cannot be ensured, even if all hole-bearing trees are retained. Ball et al. (1999) also indicated that if some of the hole-bearing trees conserved from initial logging events later die from logging-related mortality, the loss of hollow-bearing trees over time will be greatly exacerbated.

In New Zealand, many native tree species have been extensively logged in most regions until relatively recently (Griffiths 2002). The loss of hole-bearing trees is of utmost importance as *Nothofagus* spp. and many native podocarp species provide important habitat for hole-nesting bird and bat species around New Zealand (Rasch 1989; Elliott et al. 1996; Kneegtmans & Powlesland 1999; Greene 2003; Sedgely & O'Donnell 2004; Sedgely 2006). Although large-scale clearfelling and selective logging are no longer practised on New Zealand's conservation lands, there is a long legacy of historical logging and many private landowners can still remove native trees indiscriminately (Griffiths 2002), making it all the more important to quantify the abundance, distribution and structural characteristics of tree holes on *Nothofagus* and podocarp species. Thus, the purpose of this paper is to present the first comprehensive and systematic investigation of the frequency and spatial distribution of tree holes within a temperate broad-leaf-podocarp rain forest in New Zealand. Specifically, we investigated variation in the abundance, distribution and structural characteristics of tree holes with respect to: (1) variation among five endemic tree species from two common families (Fagaceae and Podocarpaceae) and (2) variation in individual tree traits (tree height and diameter).

Methods

Study site

This study was undertaken in a southern temperate broad-leaf-podocarp rain forest within Orikaka Ecological Area, Buller District, South Island, New Zealand. Orikaka Ecological Area is part of the largest continuous forest remaining in New Zealand today, at over one million hectares in extent (Fig. 1). The study area was approximately 1000 m north-west of the convergence

of the Orikaka and Buller rivers, at c. 80 m a.s.l. (41°27' S, 171°25' E) (Fig. 1). A humid, maritime, cool temperate climate is characteristic of this region. Mean annual precipitation is 2838 mm, while mean annual air temperature ranges from 8.0 to 16.5°C, with winter minimum and summer maximum temperatures of -1.0°C and 25.0°C, respectively (National Institute of Water and Atmospheric Research 2008). The nearest climate station recording sunshine hours is c. 30 km west of the study site in Westport, and these data suggest that Orikaka might receive around 1843 sunshine hours annually (National Institute of Water and Atmospheric Research 2008).

The Orikaka Ecological Area is geologically diverse, with limestone, siltstone, quartz, glacial outwash and coal measures throughout, and includes the catchments of numerous creeks and rivers as well as some wetland areas in the south. Orikaka forest covers a series of ridges and intervening basins lying between 60 and 600 m altitude. The forest canopy is dominated by *Nothofagus fusca* and *N. menziesii*, with *N. truncata* at higher elevations, and emergent *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, *P. taxifolia* and

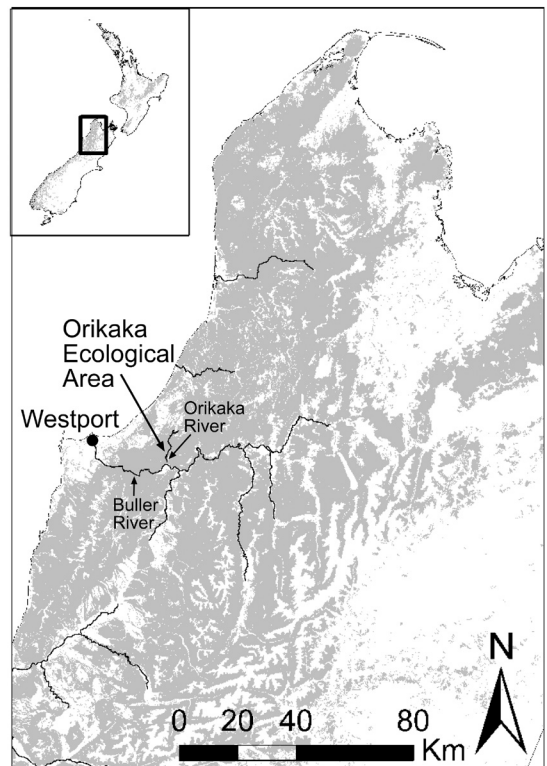


Figure 1. Location of Orikaka Ecological Area, Buller District, situated within continuous indigenous forest (grey shading) 30 km east of Westport, South Island, New Zealand.

Metrosideros robusta throughout. The understorey is dominated by *Pseudowintera colorata*, *Carpodetus serratus*, *Dicksonia squarrosa*, *Weinmannia racemosa*, *Nothofagus* seedlings, *Pseudopanax crassifolius*, *Griselinia littoralis*, *Fuchsia excorticata*, and a dense ground layer of ferns.

Approximately 1000 ha of Orikaka Ecological Area have been logged previously for podocarp and *Nothofagus* spp., but *Dacrycarpus dacrydioides* and *Prumnopitys ferruginea* were protected from commercial logging in this region (Dalley & Richards 1998). Small areas of forest have also been modified by coal mining activities and an electricity transmission line crosses the south-western corner of Orikaka. However, more than 80% of the forest remains largely unmodified by logging or mining, and Park & Walls (1978) identified parts of Orikaka Ecological Area as important representative stands of tall lowland forest in the Nelson Land District.

Tree-hole survey

A 1.96-ha portion of the Orikaka study area, unmodified by Timberland's recent forestry practices, was subdivided into 196 contiguous subplots (10 × 10 m) for systematic sampling. The 1.96-ha plot was established by randomly selecting a starting point, the south-western corner, and then measuring 140 m in both a northerly and an easterly direction to create a square. Within this 1.96-ha plot, 5–25 trees of each of *Nothofagus fusca* ($n = 25$), *N. menziesii* ($n = 10$) (Family Fagaceae), *Dacrycarpus dacrydioides* ($n = 5$), *Prumnopitys ferruginea* ($n = 5$) and *P. taxifolia* ($n = 5$) (Family Podocarpaceae) were randomly selected and surveyed for tree holes in January 2006 using single-rope climbing techniques (Barker & Standridge 2002). Climbable trees (i.e. ≥ 20 cm trunk diameter at breast height (dbh; 1.4 m) with multiple large branches in the upper canopy were selected using a random walk, beginning at the south-eastern corner of the 1.96-ha study area. Each tree was selected by generating a random compass bearing and walking a random number of metres (1–60, using the seconds hand on a watch), following which the nearest climbable tree, of any of the five tree species, was selected until the full sample of each species had been climbed. If the random walk took the arborists outside the study plot, or no climbable trees were available at the selected point, a new random bearing and distance were generated. Using a modified cross-bow, a climbing rope was positioned at the highest possible point within each tree and, subsequently, the trunk and all branches of each tree were systematically surveyed for holes.

Tree size (dbh; cm) was measured for each climbed tree. Where trees had multiple stems at breast height, the dbh was taken below the initial stem split. We also recorded the height (m), location (branch, trunk or fork) and aspect (N, S, E or W) of each individual tree hole on all climbed trees. Tree holes were recorded only if they were ≥ 1 cm in entrance height, width or horizontal depth

and penetrated at least into the outer sapwood, rather than simply representing a deformation in the tree bark (following Blakely et al. 2008). The internal (vertical and horizontal depths; cm) and external dimensions (height and width; cm) were also recorded for each tree hole. From these measurements, we calculated the entrance size (hole opening; cm²) and volume (cm³) of each tree hole using standard formulas, where tree holes were treated as ellipses. Entrance angle (degrees from vertical) was also recorded for each tree hole, with vertical holes being recorded as 0°, holes overhanging and facing towards the ground recorded as negative angles, and those facing upwards recorded as positive angles.

The presence of standing water, versus damp or dry conditions (an internal condition considered important for tree-hole-inhabiting fauna), was recorded in early December 2004 and 2006. Rainfall in Orikaka Ecological Area is fairly constant both interannually and throughout the year, with slightly lower values during January–March (long-term data, 1971–2000; National Institute of Water and Atmospheric Research 2008). Furthermore, we recorded consistent rainfall levels near our study area in November and December from 2004 to 2006. Therefore, even though the internal conditions in tree holes were measured only at two discrete time periods, we expect that this was representative of the presence of standing water in the study area, except perhaps for the hottest periods in midsummer. Lip size (cm) at the lower edge of each tree hole was also recorded, as this was considered to be a possible determinant of microclimatic conditions inside the hole (e.g. ability to retain standing water).

In order to make predictions about the number of tree holes per hectare in our study area we also recorded tree species and dbh for all canopy trees ≥ 20 cm dbh in a subset of 100 randomly selected subplots (10 × 10 m), in January 2005. This gave us size–frequency distribution information for all canopy trees (≥ 20 cm dbh) in 1 ha of our 1.96-ha study area.

Statistical analyses

Analysis of covariance (ANCOVA) was used to explore the main and interactive effects of tree species and size (dbh) on the number of tree holes identified during the climbed inspections. We used linear mixed-effects (LME) models (using the *lmer* package in R; R Foundation 2007) tested with maximum likelihood (ML) to explore the amount of variation in tree-hole volume (cm³) and hole opening (cm²) explained by the fixed effect of tree species (*N. fusca*, *N. menziesii*, *D. dacrydioides*, *P. ferruginea* and *P. taxifolia*) and the fixed covariate effect of tree size (dbh), while accounting for the random effect of variation in hole size among individual trees (tree identity), nested within tree species. Nested mixed-effects models were used because of the hierarchical design of the survey in which there was dependence among individual holes within trees. Thus, hole volumes and openings within trees were not

treated as independent replicates, but were nested within tree species to avoid pseudoreplication (Crawley 2007). We used model simplification to estimate the P values and test the significance of tree species, dbh, and their interaction (Crawley 2007). That is, the fixed effects of tree species and dbh, as well as their interaction, were removed one by one from the LME models and using ML we were able to estimate the chi-square (χ^2) statistic and its significance level for each of the predictors, and their interaction.

Pearson's correlations were used to test if tree size (dbh) and mean tree-hole characteristics per tree, such as mean hole opening, internal volume or hole height above ground, were linearly related. Pearson's correlations were also used to test if these three tree-hole characteristics were linearly related to each other, independent of tree dbh. Chi-square contingency tables were used to determine whether tree holes were equally distributed amongst branches and trunks, or if they were more likely to occur on N, E, S or W aspects, for the five tree species surveyed. Chi-square contingency tables were also used to test separately whether the internal condition of tree holes (i.e. wet vs dry) was influenced by tree species, hole aspect, location, entrance angle, or lip size. Entrance angles were pooled together into three categories (vertical, upwards, or downwards facing) while lip sizes were combined into four arbitrarily assigned size categories (0–0.9, 1–4.9, 5–9.9 or ≥ 10 cm). Tree holes in branch forks were excluded from the analyses and tree holes containing standing water were combined with damp holes to meet the recommended statistical assumption that no more than 20% of the categories had expected frequencies of less than five.

All analyses were performed in R version 2.6.0 (R Foundation 2007). Response and predictor variables were $\ln(x+1)$ transformed where necessary to meet assumptions of normality and homogeneity of variances.

Results

The ground-vegetation survey of 100 randomly selected subplots (10 × 10 m) within the 1.96-ha Orikaka study area indicated that *Nothofagus fusca* and *N. menziesii* were the most abundant canopy tree species (53% and 34%, respectively; Table 1). Although present in the study area, *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea* and *P. taxifolia* were much less common in the canopy, together making up just 13% of canopy trees in the 1-ha area surveyed (Table 1).

In total, 364 tree holes were recorded on the 50 sampled trees in Orikaka Ecological Area. Furthermore, 96% of these climbed trees were hole-bearing, with only one of each of *Nothofagus fusca* and *N. menziesii* having no tree holes. The 50 climbed trees were highly variable in size (46.5–136.0 cm dbh), but there was no significant difference in average tree size across the five tree species ($F_{4,45} = 0.40$, $P = 0.890$). There were many more holes in large trees than in small trees ($F_{1,44} = 5.12$, $P = 0.029$; Fig. 2), but more importantly the effect of tree size (dbh) on tree-hole abundance was consistent across the five tree species ($F_{4,40} = 1.01$, $P = 0.415$; Fig. 2). The three podocarp species had more holes per tree than either of the *Nothofagus* species ($F_{4,44} = 3.85$, $P = 0.009$; Fig. 2). *Prumnopitys ferruginea* had the most holes per tree (15.2 ± 3.0 , $n = 5$), followed by *P. taxifolia* (8.6 ± 2.0 , $n = 5$), *Dacrycarpus dacrydioides* (7.8 ± 3.0 , $n = 5$), *Nothofagus fusca* (6.8 ± 0.8 , $n = 25$), and *N. menziesii* (3.7 ± 1.0 , $n = 10$).

We measured the internal dimensions on 354 of the 364 tree holes identified during the climbed inspections. Tree-hole volume varied markedly among these 354 holes, from the smallest measurable hole of only 0.5 cm^3 up to the largest, six orders of magnitude greater, at more than 0.157 m^3 . However, the majority (83%) of holes on all

Table 1. Total number of canopy trees ≥ 20 cm dbh (diameter at breast height, 1.4 m) and the percentage that each species contributes to four arbitrarily assigned size classes within 100 randomly selected subplots (10 × 10 m) surveyed inside Orikaka Ecological Area, Buller District, New Zealand, in January 2006.

Tree species	N	Trees in dbh (cm) class (%)				Trees per hectare (%)
		20–20.9	30–30.9	40–40.9	≥ 50	
<i>Nothofagus fusca</i>	101	12	12	11	65	53
<i>Nothofagus menziesii</i>	65	29	23	11	37	34
<i>Prumnopitys ferruginea</i>	14	29	21	00	50	7
<i>Prumnopitys taxifolia</i>	9	33	11	11	45	5
<i>Dacrycarpus dacrydioides</i>	2	0	0	50	50	1
<i>Dacrydium cupressinum</i>	1	0	0	0	100	1

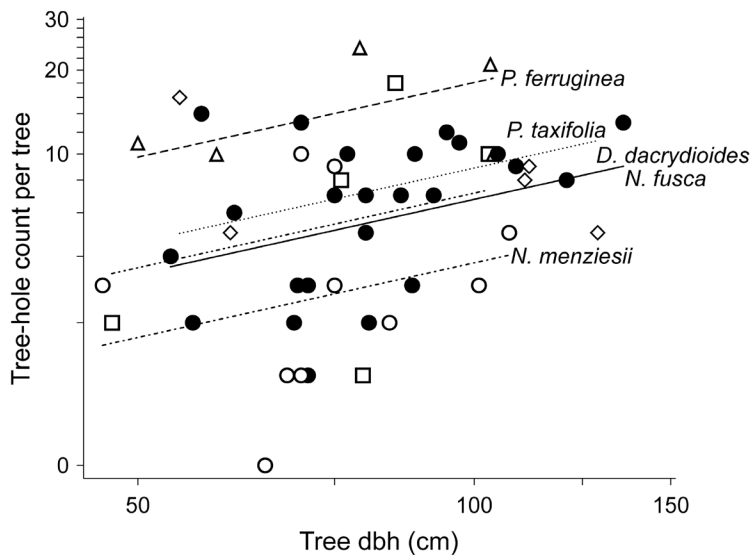


Figure 2. Variation in tree hole number recorded during climbed inspections on *Nothofagus fusca* (● and solid fitted line, $n = 25$), *N. menziesii* (○ and dash-dot fitted line, $n = 10$), *Dacrycarpus dacrydioides* (□ and dash-dot-dot fitted line, $n = 5$), *Prumnopitys ferruginea* (△ and dashed fitted line, $n = 5$) and *P. taxifolia* (◇ and dotted fitted line, $n = 5$) of differing sizes (dbh) climbed in Orikaka Ecological Area, Buller District, New Zealand, in January 2006. Note that the y-axis is plotted on a logarithmic scale. The fitted lines [$\ln(y)$] equal: $-1.769 + 0.829 \cdot \ln(x)$ (*N. fusca*), $-2.258 + 0.829 \cdot \ln(x)$ (*N. menziesii*), $-1.721 + 0.829 \cdot \ln(x)$ (*D. dacrydioides*), $-0.869 + 0.829 \cdot \ln(x)$ (*P. ferruginea*) and $-1.528 + 0.829 \cdot \ln(x)$ (*P. taxifolia*).

tree species were small (0–999-cm³ volumes). Although *Nothofagus fusca* had significantly fewer tree holes than all three podocarp species, tree holes on *N. fusca* were much larger, on average, than all other tree species (Fig. 3). There was a significant effect of tree species on hole volume ($\chi^2_4 = 11.64$, $P = 0.020$), while the tree dbh covariate also significantly affected hole volume ($\chi^2_1 = 29.45$, $P < 0.001$; Fig. 3a). The effect of dbh did not vary across the five tree species ($\chi^2_4 = 4.42$, $P = 0.353$), indicating that the increase in hole volume with increasing tree size or age was consistent among these tree species (Fig. 3a).

Although there was a slight trend for *Nothofagus fusca* to have larger hole openings, there was no overall effect of tree species on hole entrance size ($\chi^2_4 = 8.45$, $P = 0.076$; Fig. 3b). There was, however, a significant effect of tree dbh on hole opening, with larger trees having substantially larger hole openings ($\chi^2_1 = 21.96$, $P < 0.001$). In this case, the increase in tree-hole entrance with increasing tree dbh was consistent among the five tree species ($\chi^2_4 = 5.12$, $P = 0.276$) (Fig. 3b).

Tree dbh was positively correlated with both mean hole opening ($r = 0.70$, $P < 0.001$) and mean hole volume ($r = 0.58$, $P < 0.001$) per tree, with larger trees of all species having bigger holes. However, holes situated higher off the ground tended to have smaller openings on *Nothofagus menziesii* and *Prumnopitys ferruginea* (hole height and hole entrance correlations: $r = -0.36$, $P = 0.031$ and $r = -0.35$, $P = 0.002$, respectively), and holes high up on *Dacrycarpus dacrydioides* and *P. ferruginea* had smaller hole volumes ($r = -0.38$, $P = 0.016$ and $r = -0.31$, $P = 0.006$, respectively).

Hole entrance size was strongly, positively correlated with its internal hole volume ($r = 0.69$, $P < 0.001$; Fig. 4). This was true for all tree species, with large tree holes (internally) generally having greater openings. However, the relationship between hole opening and volume was more variable on *Nothofagus fusca* ($r = 0.65$, $P < 0.010$; Fig. 4a) and *N. menziesii* ($r = 0.53$, $P = 0.001$; Fig. 4b) trees, compared with *Dacrycarpus dacrydioides* ($r = 0.81$, $P < 0.001$; Fig. 4c), *Prumnopitys ferruginea* ($r = 0.74$, $P < 0.001$; Fig. 4d) and *P. taxifolia* ($r = 0.70$, $P < 0.001$; Fig. 4e).

Although tree holes were evenly distributed between trunks (48%) and branches (52%) overall, the relative spatial distribution of holes varied among tree-species ($\chi^2_4 = 20.48$, $P < 0.001$; Table 2). Tree holes were also non-randomly distributed on different aspects of trees ($\chi^2_{12} = 27.26$, $P = 0.007$; Table 2).

Only 2% of all the tree holes inspected contained standing water suitable for aquatic fauna to inhabit, while a further 18% were damp at the time of sampling. Thus, 20% of all holes contained some moisture (i.e. potentially containing water at times); the remaining 80% of tree holes were dry inside in December 2004 and 2006. Entrance angle (positive or negative angle, or 0°) was not a significant determinant of the internal conditions of these tree holes (i.e. damp or dry) ($\chi^2_2 = 4.37$, $P = 0.112$). Few tree holes (20%) faced downwards (negative entrance angle) and the majority either faced directly out from the vertical face of the tree (45% at an angle of 0°) or were upwards facing (35%). Similarly, there was no clear relationship between internal dampness and hole aspect ($\chi^2_3 = 5.62$,

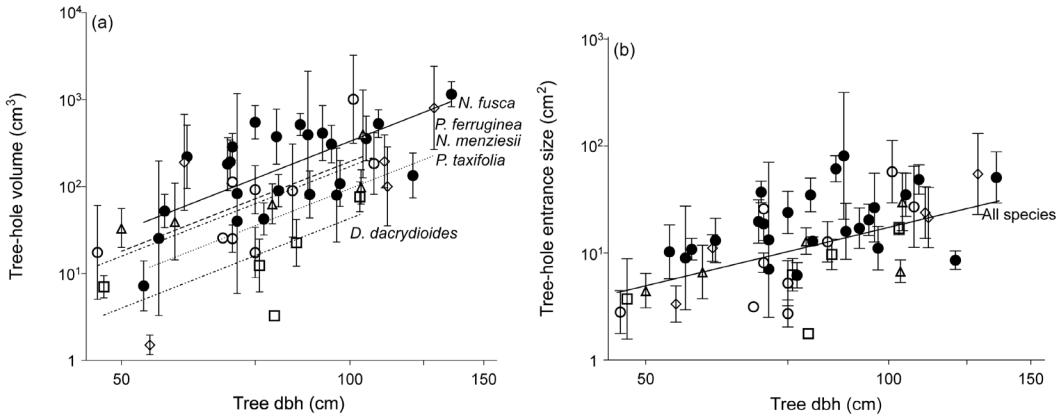


Figure 3. Variation in mean (\pm SE) tree-hole (a) volume and (b) entrance size per tree recorded on *Nothofagus fusca* (\bullet and solid fitted line, $n = 24$), *N. menziesii* (\circ and dash-dot fitted line, $n = 9$), *Dacrycarpus dacrydioides* (\square and dash-dot-dot fitted line, $n = 5$), *Prumnopitys ferruginea* (\triangle and dashed fitted line, $n = 5$) and *P. taxifolia* (\diamond and dotted fitted line, $n = 5$) of differing sizes (dbh) climbed in Orikaka Ecological Area, Buller District, New Zealand, in January 2006. Note that there was no significant effect of species on (b) hole entrance size, so the solid line indicates a common slope for all species. The y -axes are plotted on logarithmic scales. The fitted lines [$\ln(y)$] for (a) tree-hole volume equal: $-9.998 + 3.432 \cdot \ln(x)$ (*N. fusca*), $-10.667 + 3.432 \cdot \ln(x)$ (*N. menziesii*), $-12.042 + 3.432 \cdot \ln(x)$ (*D. dacrydioides*), $-10.536 + 3.432 \cdot \ln(x)$ (*P. ferruginea*) and $-11.251 + 3.432 \cdot \ln(x)$ (*P. taxifolia*). Equation of fitted line for (b) tree-hole entrance size is: $\ln(y) = -5.491 + 1.812 \cdot \ln(x)$.

Table 2. Relative abundance (%) of tree holes located on trunks or branches and on different aspects of tree species of differing sizes (dbh) climbed in Orikaka Ecological Area, Buller District, New Zealand, in January 2006.

Tree species	No. sampled	Total no. tree holes	Location		Aspect			
			Trunk	Branch	North	South	East	West
<i>Nothofagus fusca</i>	25	169	59	41	14	25	30	31
<i>Nothofagus menziesii</i>	10	37	27	73	19	33	16	32
<i>Dacrycarpus dacrydioides</i>	5	39	56	44	41	16	10	33
<i>Prumnopitys ferruginea</i>	5	76	40	60	13	17	33	37
<i>Prumnopitys taxifolia</i>	5	43	33	67	20	26	21	33

$P = 0.132$), lip size ($\chi^2_3 = 4.76$, $P = 0.190$) or location on the tree ($\chi^2_1 = 0.69$, $P = 0.406$). There was, however, significant variation in the proportion of damp or water-filled holes among tree species ($\chi^2_3 = 9.80$, $P = 0.020$). Just 3% of tree holes on *Dacrycarpus dacrydioides* were either water-filled or damp, while 13% of *Prumnopitys ferruginea* holes were wet compared with much higher proportions for *Nothofagus fusca* (22%), *P. taxifolia* (30%) and *N. menziesii* (30%).

Discussion

Concurrent work in mixed broad-leaf-podocarp forest within Orikaka Ecological Area (this study) and within

Nothofagus spp. forest in the Lewis Pass (Blakely et al. 2008) indicates that previous researchers have dramatically underestimated the abundance of tree holes in native forests around New Zealand (Table 3). Nearly all trees in this study and in the Lewis Pass (Blakely et al. 2008) were hole-bearing ($\geq 90\%$), compared with previous studies where, at most, 60% of trees were reported to be hole-bearing (Table 3). Of course, it is important to consider that tree-hole abundance is likely to be strongly dependent on local climatic differences, forest stand age, disturbance history, and pathogen abundance. Thus, the abundance of tree-holes may naturally vary to some degree between forest sites. For example, in Orikaka Ecological Area, *Nothofagus fusca* had 10-fold more tree holes and *N. menziesii* more than 5-fold the number of holes reported

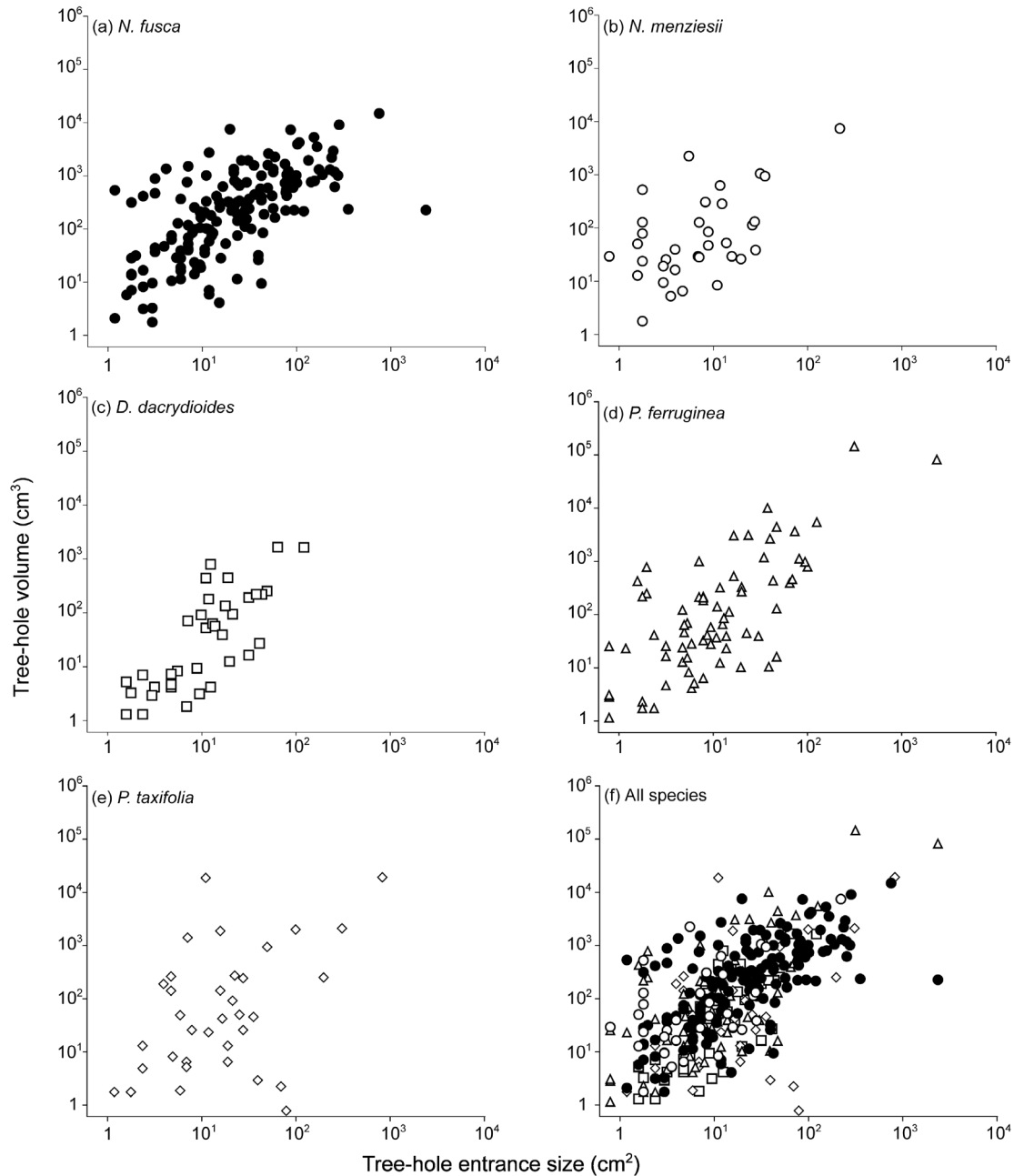


Figure 4. Relationship between entrance size (cm²) of tree holes and tree-hole volume (cm³) for (a) *Nothofagus fusca* (●, $n = 162$), (b) *N. menziesii* (○, $n = 35$), (c) *Dacrycarpus dacrydioides* (□, $n = 39$), (d) *Prumnopitys ferruginea* (△, $n = 75$), (e) *P. taxifolia* (◇, $n = 43$) and (f) all tree species ($n = 354$) climbed in Orikaka Ecological Area, Buller District, New Zealand, in January 2006.

Table 3. Percentage of hole-bearing trees and mean number of holes per tree compared between studies in *Nothofagus* and mixed broad-leaf-podocarp forests, New Zealand.

Tree species	No. trees in sample	Hole-bearing trees (%)	Mean no. holes per tree	Minimum hole entrance size (cm)
<i>Nothofagus fusca</i> ¹	25	96†	6.8	1.0
<i>N. fusca</i> ²	10	100†	17.4	1.0
<i>N. fusca</i> ³	358	45‡	0.7	1.3
<i>Nothofagus menziesii</i> ¹	10	90†	3.7	1.0
<i>N. menziesii</i> ²	10	100†	8.1	1.0
<i>N. menziesii</i> ³	136	21‡	0.7	1.3
<i>Prumnopitys ferruginea</i> ¹	5	100†	15.2	1.0
<i>Prumnopitys taxifolia</i> ¹	5	100†	8.6	1.0
<i>Dacrycarpus dacrydioides</i> ¹	5	100†	7.8	1.0
Podocarp-hardwood species* ⁴	188	16‡	0.4	1.3

¹This study; ²Blakely et al. (2008); ³Sedgeley & O'Donnell (1999b); ⁴Sedgeley (2006). *Comprising *Podocarpus hallii*, *Weinmannia racemosa*, *Prumnopitys ferruginea*, *Dacrydium cupressinum*, *Metrosideros umbellata*, *Griselinia littoralis*, *Leptospermum scoparium* and dead trees of these; † direct inspections (e.g. climbed inspections); ‡ ground-based surveys using binoculars.

for the same tree species in previous work conducted at the same level of sampling intensity (cf. Table 3 and Blakely et al. 2008). For the most part, the main reason earlier studies have underestimated tree-hole density in New Zealand forests is that they have relied on ground-based surveys of tree holes and focused primarily on the trunk and lower branches, or have indirectly quantified tree-hole abundance by tracking obligate hole-dwelling vertebrate species (e.g. Sedgeley & O'Donnell 1999b; Sedgeley 2003, 2006). However, New Zealand's native hole-nesting bird and bat species often select tree holes with very specific dimensions (Elliott et al. 1996; Sedgeley & O'Donnell 1999b; Greene 2003; Sedgeley 2003), and consequently previous work has been biased towards recording larger holes suitable for these hole-dwelling vertebrate species. Yet, the majority of tree holes are actually very small (83% of all holes were < 999 cm³) and our data indicate that results from these previous studies (Table 3) do not fairly represent the true underlying distribution of all tree holes from which vertebrate and invertebrate species are selecting habitat.

Frequency, distribution and formation of tree holes

Tree size had an important influence on tree-hole abundances, with larger (and older) trees having many more tree holes. These holes were also bigger, both inside and out. Tree species also had an important effect on the abundance, distribution and structural characteristics of tree holes. The three podocarp species had many more tree holes per tree than either *Nothofagus fusca* or *N. menziesii* at this site. In fact, *Prumnopitys ferruginea*

had more than twice as many tree holes as *Nothofagus fusca*, and more than four times the number of holes per tree as *N. menziesii*. This marked effect of tree species on hole abundances could result from a range of different processes, including differential growth rates among species. For instance, podocarp species are typically slower growing than *Nothofagus* spp. (e.g. Lusk & Smith 1998), and within *Nothofagus* species *N. fusca* is typically slower growing than *N. menziesii* (Wardle 1984). Thus, in areas of equivalent site productivity, *Prumnopitys ferruginea*, *P. taxifolia* or *Dacrycarpus dacrydioides* trees of a given diameter are likely to be older than *Nothofagus fusca* or *N. menziesii* trees of the same size, and may therefore contain more holes due to age rather than size, per se (Lindenmayer et al. 1993; Gibbons & Lindenmayer 2002).

It is also plausible that the observed variation in the distribution and abundance of tree holes among species may be related to differences in wood density, as tree species with lower wood densities are probably more susceptible to branch breakage. Wood density is the single most important factor determining mechanical breaking strength (Persson et al. 1995; Beets et al. 2001) and can be highly variable across different tree species. The timber densities of *Nothofagus fusca*, *N. menziesii*, *Prumnopitys ferruginea* and *P. taxifolia* are similar (c. 590–630 kg m⁻³), while timber of *Dacrycarpus dacrydioides* is only slightly less dense (450 kg m⁻³) (Wardle 1984; Timbers of New Zealand Ltd 2007), suggesting that *D. dacrydioides* should be more susceptible to branch breakage and subsequent tree-hole formation. However, although *Prumnopitys ferruginea* and *P. taxifolia* are known to have extremely

strong timber, they can also be very brittle (Hay & Dellow 1952). This may potentially cause these podocarp species to experience greater branch breakage frequency, and therefore greater tree-hole formation rates, than the *Nothofagus* species in this study.

By contrast, although hole-formation rates may be high in podocarp trees, it is possible that the natural durability of their timber may limit hole-expansion rates. For example, Gibbons & Lindenmayer (2002) suggested that many tree holes form when heartwood decay is already present and a tree is subsequently exposed to some form of physiological or physical stress. Therefore, if some species are more susceptible to branch breakage due to comparatively lower breaking strengths or brittleness, more tree holes might form in the outer sapwood. But many podocarp species contain high levels of chemical defences (e.g. Bauch et al. 2006), thereby potentially providing heartwood with some level of protection from fungal decay and rot.

Consistent with the hypothesis of differences in susceptibility to rot, Blakely et al. (2008) found that *Nothofagus fusca* in the Lewis Pass had many more, larger tree holes than *N. menziesii* and *N. solandri* (mountain beech) and inferred that these findings were a reflection of the differences in timber properties and the associated susceptibility to rot and attack by decay-causing organisms. Thus, despite the fact that the *Nothofagus* spp. had fewer tree holes per tree than the podocarp species surveyed, the timber durability of these podocarp species might partially explain why they have smaller tree holes than *N. fusca* in Orikaka Ecological Area.

Implications for management

In the past, numerous studies from around New Zealand have used ground-based surveys to quantify the number of holes suitable for hole-dwelling fauna by scanning trees with binoculars (e.g. Sedgeley & O'Donnell 1999b; Sedgeley 2006). However, in the Lewis Pass region, Blakely et al. (2008) found that ground-based surveys consistently underestimated the abundance of tree holes in pure *Nothofagus* forest, when compared with tree-hole counts obtained during climbed inspections. In fact, less than 10% of the tree holes on any given tree could be identified from the ground, and those situated higher off the forest floor were the hardest to detect (Blakely et al. 2008). Of course, the argument could be made that the holes missed in ground surveys are also the smallest tree holes and therefore the least likely to be important for many of New Zealand's hole-dwelling birds and bats (e.g. Elliott et al. 1996; Sedgeley & O'Donnell 1999a; Greene 2003). This is true to an extent (although small tree holes are also important for invertebrate biodiversity), therefore it is of great interest that we found tree-hole opening to be significantly positively correlated with tree-hole volume, potentially making entrance size a useful external predictor of internal hole dimensions. Thus rapid, cost-effective,

ground-based surveys of tree-hole entrance size could be a useful management approach for quantifying the abundance of large tree holes that are most likely to be suitable for specific hole-dwelling fauna, particularly if ground surveys are calibrated intermittently with climbed inspections. However, it is important to note that although tree-hole entrance size was significantly correlated with tree-hole volume in Orikaka Ecological Area, the strength of this relationship varied among tree species. For example, tree holes with large openings in *Nothofagus fusca* and *N. menziesii* typically had larger volumes, but this was not always the case. Some tree holes we measured in *Nothofagus* spp. trees were very large internally, but had small hole openings, leading to high variance around the observed relationship. In contrast, there was a much more predictable relationship between hole volume and entrance size on tree holes measured on *Dacrydium dacrydioides*, and to a lesser extent *Prumnopitys ferruginea* and *P. taxifolia*.

Extrapolating tree-hole densities

By extrapolating from the average number of holes recorded on tree species within each of four arbitrarily assigned size classes (20–29.9, 30–39.9, 40–49.9 >50 cm dbh), multiplied by the relative frequency of trees of that size present in a 1-ha area of the study plot, we estimated that there might be as many as 771 tree holes per hectare of forest at this site. It is possible that even this high density of tree holes might be an underestimate as not all tree species present in Orikaka Ecological Area were surveyed. Furthermore, although the utmost care was taken to survey each tree in its entirety, tree holes on the outer-most edges of large canopy branches may have been missed.

We also estimated that 'large', dry tree holes suitable for solitary lesser short-tailed and long-tailed bats (minimum entrance 1.3×2.7 cm, volume ≥ 23 cm³, and situated ≥ 5 m off the forest floor; Sedgeley & O'Donnell 1999a; Sedgeley 2003) may be very common in our study area. In fact, we predicted that there might be as many as 384 tree holes per hectare available for native bats, and *Nothofagus fusca* was estimated to harbour 76% of these. Nevertheless, these bat species have very specific habitat requirements (Sedgeley & O'Donnell 1999a) and it is likely that fewer tree holes provide habitat suitable for colonies of lesser short-tailed and long-tailed bats.

Dry tree holes available for mohua and yellow-crowned kakariki nests (minimum entrance dimension 2.5 cm, minimum internal dimension ≥ 15 cm, and situated ≥ 14 m off the forest floor; Elliott et al. 1996) were relatively uncommon in our study area, with an estimate of as few as 14 holes per hectare. However, it is important to remember that this study was conducted in a relatively small area, so estimates such as these need to be treated with caution. Moreover, it is important to point out that tree-hole abundance and size were strongly

dependent on both tree species and dbh and is therefore likely to differ throughout New Zealand. For example, tree holes were estimated to be far more abundant (3906 holes per hectare) in continuous old-growth *Nothofagus* forest in the Lewis Pass just 60 km away (Blakely et al. 2008). Holes for native bats were also more abundant in the Lewis Pass (963 holes per hectare), than at Orikaka, whereas estimates of the number of holes for mohua and yellow-crowned kakariki were more comparable with just eight holes estimated per hectare in Lewis Pass (Blakely et al. 2008).

The presence of standing water plays an integral role in determining the composition of tree-hole communities, supplying resources for highly specialised aquatic invertebrate communities (Kitching 1971). However, very little is known about water-filled tree holes or the communities they support in New Zealand (but see Derraik & Heath 2005). In this study, there were marked differences in internal conditions of the tree holes across tree species. Unlike *Dacrycarpus dacrydioides*, and to a lesser extent *Prumnopitys ferruginea*, where the vast majority of tree holes were dry at the time of sampling, a large proportion of tree holes on *Nothofagus menziesii*, *N. fusca* and *P. taxifolia* were either water-filled or damp. Although only 2% of tree holes contained standing water, a further 18% were damp inside, indicating that as many as 20% of holes may collect rainwater via stemflow at times. Therefore, despite the low proportion of water-filled tree holes encountered at the time of sampling, we estimate there could be as many as 144 holes per hectare that retain standing water for a period of time, providing important, albeit ephemeral, resources for a multitude of aquatic and semi-aquatic invertebrate species (Kitching 1971; Yanoviak 2001; Taylor & Ewers 2003; T.J. Blakely unpubl. data).

Deforestation and selective logging

Deforestation and selective logging are known to greatly influence the distribution of hole-bearing trees and in turn the abundance of tree holes (Ball et al. 1999; Graves et al. 2000; Gibbons & Lindenmayer 2002). Many of New Zealand's obligate hole-dwelling species, in particular mohua, yellow-crowned kakariki and long-tailed bats (all of which nest in large, hole-bearing trees), have almost certainly been greatly impacted by the large-scale removal of forest throughout New Zealand, exacerbated by predation from exotic species (O'Donnell 1996; Sedgeley & O'Donnell 2004). Large-scale logging of native forest is no longer practised in New Zealand, but historically, Orikaka Ecological Area was subject to commercial logging, and both *Nothofagus* and podocarp species were harvested from approximately 1000 ha of forest (Dalley & Richards 1998). At this time, silviculture aimed to perpetuate an even-aged forest structure, where trees were generally removed after 60–120 years before they reached a large size (<75 cm dbh) (Wardle 1984).

Clearly, the direct loss of hole-bearing trees due to their removal for timber, coupled with the reduction in future hole-bearing cohorts, may have dire impacts on obligate hole-dwelling fauna, as has been shown for many vertebrate and invertebrate species overseas (O'Donnell 1991; Graves et al. 2000; Ranius 2002). Indeed, modified forests, with fewer medium- and large-sized trees, have disproportionately fewer hole-bearing trees than unmodified forests (Mackowski 1984; Lindenmayer et al. 1991; Newton 1994; Kirby et al. 1998; Gibbons & Lindenmayer 2002).

Conclusions

This is the first systematic survey of the distribution of tree-hole microhabitats for a range of *Nothofagus* and podocarp tree species in New Zealand. All tree species surveyed in Orikaka Ecological Area provided tree holes of a variety of sizes, heights and volumes, and for some tree species the frequencies of holes per tree were among the highest ever recorded in a New Zealand forest (Table 3) and worldwide (Blakely et al. 2008). These tree holes are likely to support a diverse array of vertebrate and invertebrate fauna in this temperate-rain-forest environment. This is particularly important for the conservation management of hole-dwelling birds and bats in New Zealand, because even though detailed information is available on habitat requirements (e.g. Elliott et al. 1996; Greene 2003; Sedgeley & O'Donnell 1999a; Sedgeley 2003), little work has been done to map the spatial distribution of suitable tree-hole microhabitats within, and beyond, the current distributions of these endangered species. Knowledge of this kind could be particularly important when conservation managers are investigating species reintroduction and attempting to quantify the abundance and distribution of available hole microhabitats. Finally, sustainable logging of native forests is a controversial issue in New Zealand (Norton 2000; Wilson & Memon 2005), and there has been little thought given to the disproportionate impact that the removal of medium- to large-sized hole-bearing trees might have on the long-term distribution of tree holes and the hole-nesting fauna these unique microhabitats support.

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References

- Ball IR, Lindenmayer DB, Possingham HP 1999. A tree hollow dynamics simulation model. *Forest Ecology and Management* 123: 179–194.
- Barker M, Standridge N 2002. Ropes as a mechanism for canopy access. In: Mitchell AW, Secoy K, Jackson T eds. *The global canopy handbook: techniques of access and study in the forest roof*. Oxford, Global Canopy Programme. Pp. 13–23.
- Bauch J, Koch G, Puls J, Schwarz T, Voiß S 2006. Wood characteristics of *Podocarpus oleifolius* var. *macrostachyus* (Parl.) Buchholz and Gray native to Costa Rica: their significance for wood utilization. *Wood Science and Technology* 40: 26–38.
- Beets PN, Gilchrist K, Jeffreys MP 2001. Wood density of radiata pine: effect of nitrogen supply. *Forest Ecology and Management* 145: 173–180.
- Bennett AF, Lumsden LF, Nicholls AO 1994. Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. *Pacific Conservation Biology* 1: 222–235.
- Blakely TJ, Jellyman PG, Holdaway RJ, Young L, Burrows B, Duncan P, Thirkettle D, Simpson J, Ewers RM, Didham RK 2008. The distribution, abundance and structural characteristics of tree holes in *Nothofagus* forest, New Zealand. *Austral Ecology*, doi:10.1111/j.1442-9993.2008.01867.x.
- Crawley MJ 2007. *The R book*. Chichester, UK, Wiley.
- Dalley RJ, Richards CR 1998. Sustainable management plan for the Inangahua Working Circle forests. Greymouth, Timberlands West Coast Limited.
- Derraik JGB 2005. Mosquitoes breeding in phytotelmata in native forests in the Wellington region, New Zealand. *New Zealand Journal of Ecology* 29: 185–191.
- Derraik JGB, Heath ACG 2005. Immature Diptera (excluding Culicidae) inhabiting phytotelmata in the Auckland and Wellington regions. *New Zealand Journal of Marine and Freshwater Research* 39: 981–987.
- Elliott GP, Dilks PJ, O'Donnell CFJ 1996. Nest site selection by mohua and yellow-crowned parakeets in beech forest in Fiordland, New Zealand. *New Zealand Journal of Zoology* 23: 267–278.
- Fan Z, Shiffley SR, Spetich MA, Thompson III FR, Larsen DR 2003. Distribution of cavity trees in midwestern old-growth and second-growth forests. *Canadian Journal of Forest Research* 33: 1481–1494.
- Gibbons P, Lindenmayer D 2002. *Tree hollows and wildlife conservation in Australia*. Melbourne, Australia, CSIRO Publishing.
- Graves AT, Fajvan MA, Miller GW 2000. The effects of thinning intensity on snag and cavity tree abundance in an Appalachian hardwood stand. *Canadian Journal of Forest Research* 30: 1214–1220.
- Greene TC 2003. Breeding biology of red-crowned parakeets (*Cyanoramphus novaezelandiae novaezelandiae*) on Little Barrier Island, Hauraki Gulf, New Zealand. *Notornis* 50: 83–99.
- Greeney HF 2001. The insects of plant-held waters: a review and bibliography. *Journal of Tropical Ecology* 17: 241–260.
- Griffiths AD 2002. Indigenous forestry on private land: present trends and future potential. Ministry of Agriculture and Forestry Technical Paper No. 01/6.
- Hay JA, Dellow UV 1952. New Zealand conifers – a note on their uses and importance. *Tuatara* 4: 108–117.
- Kirby KJ, Reid CM, Thomas RC, Goldsmith FB 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology* 35: 148–155.
- Kitching RL 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *Journal of Animal Ecology* 40: 281–302.
- Kitching RL 2001. Food webs in phytotelmata: “bottom-up” and “top-down” explanations for community structure. *Annual Review of Entomology* 46: 729–760.
- Knegtmans JW, Powlesland RG 1999. Breeding biology of the North Island tomtit (*Petroica macrocephala toitoi*) at Pureora Forest Park. *Notornis* 46: 446–456.
- Lindenmayer DB, Cunningham RB, Nix HA, Tanton MT, Smith AP 1991. Predicting the abundance of hollow-bearing trees in montane forests of south-eastern Australia. *Australian Journal of Ecology* 16: 91–98.
- Lindenmayer DB, Cunningham RB, Donnelly CF, Tanton MT, Nix HA 1993. The abundance and development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management* 60: 77–104.
- Lindenmayer DB, Cunningham RB, Pope ML, Gibbons P, Donnelly CF 2000. Cavity sizes and types in Australian eucalypts from wet and dry forest types—a simple rule of thumb for estimating size and number of cavities. *Forest Ecology and Management* 137: 139–150.
- Lusk CH, Smith B 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* 79: 795–806.
- Mackowski CM 1984. The ontogeny of hollows in blackbutt (*Eucalyptus pilularis*) and its relevance

- to the management of forests for possums, gliders and timber. In: Smith AP, Hume ID eds. Possums and gliders. Sydney, Australia, Australian Mammal Society. Pp. 554–567.
- National Institute of Water and Atmospheric Research 2008. The national climate database. Wellington, NIWA. <http://cliflo.niwa.co.nz/> [accessed 18 January 2008].
- Newton I 1994. The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation* 70: 265–276.
- Norton DA 2000. Conservation biology and private land: shifting the focus. *Conservation Biology* 14: 1221–1223.
- O'Donnell CFJ 1991. Application of the wildlife corridors concept to temperate rainforest sites, North Westland, New Zealand. In: Saunders DA, Hobbs RJ eds. The role of corridors. *Nature conservation 2*. Chipping Norton, NSW, Surrey Beatty. Pp. 85–98.
- O'Donnell CFJ 1996. Predators and the decline of New Zealand forest birds: an introduction to the hole-nesting bird and predator programme. *New Zealand Journal of Zoology* 23: 213–219.
- Park GN, Walls GY 1978. Inventory of tall forest stands on lowland plains and terraces in Nelson and Marlborough land districts, New Zealand. Wellington, Botany Division, DSIR.
- Persson B, Persson A, Ståhl EG, Karlmatz U 1995. Wood quality of *Pinus sylvestris* progenies at various spacings. *Forest Ecology and Management* 76: 127–138.
- Peterson CJ 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *Science of the Total Environment* 262: 287–311.
- R Foundation 2007. The R Foundation for statistical computing. R2.6. <http://www.r-project.org>. [accessed 15 December 2007].
- Ranius T 2002. Population ecology and conservation of beetles and pseudoscorpions living in hollow oaks in Sweden. *Animal Biodiversity and Conservation* 25: 53–68.
- Rasch G 1989. Cavity nesting in stitchbirds and the use of artificial nest sites. *Notornis* 36: 27–36.
- Robertson CJR 1985. Complete book of New Zealand birds. New South Wales, Australia, Readers Digest Services.
- Sedgeley JA 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38: 425–438.
- Sedgeley JA 2003. Roost site selection and roosting behaviour in lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in *Nothofagus* forest, Fiordland. *New Zealand Journal of Zoology* 30: 227–241.
- Sedgeley JA 2006. Roost site selection by lesser short-tailed bats (*Mystacina tuberculata*) in mixed podocarp-hardwood forest, Whenua Hou/Codfish Island, New Zealand. *New Zealand Journal of Zoology* 33: 97–111.
- Sedgeley JA, O'Donnell CFJ 1999a. Factors influencing the selection of roost cavities by a temperate rainforest bat (Vespertilionidae: *Chalinolobus tuberculatus*) in New Zealand. *Journal of Zoology* 249: 437–446.
- Sedgeley JA, O'Donnell CFJ 1999b. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. *Biological Conservation* 88: 261–276.
- Sedgeley JA, O'Donnell CFJ 2004. Roost use by long-tailed bats in South Canterbury: examining predictions of roost-site selection in a highly fragmented landscape. *New Zealand Journal of Ecology* 28: 1–18.
- Stewart GH, Burrows LE 1994. Coarse woody debris in old-growth temperate beech (*Nothofagus*) forests of New Zealand. *Canadian Journal of Forest Research* 24: 1989–1996.
- Taylor RC, Ewers RM 2003. The invertebrate fauna inhabiting tree holes in a red beech (*Nothofagus fusca*) tree. *The Weta: News Bulletin of the Entomological Society of New Zealand* 25: 24–27.
- Timbers of New Zealand Limited 2007. http://www.timbers.co.nz/index_files/Page993.htm [accessed 20 December 2007].
- Wardle JA 1984. The New Zealand beeches: ecology, utilization, and management. Christchurch, New Zealand, New Zealand Forest Service.
- Whitford KR 2002. Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees I. Hollow sizes, tree attributes and ages. *Forest Ecology and Management* 160: 201–214.
- Wilson GA, Memon PA 2005. Indigenous forest management in 21st-century New Zealand: towards a 'postproductivist' indigenous forest-farmland interface? *Environment and Planning A* 37: 1493–1517.
- Yanoviak SP 2001. The macrofauna of water-filled tree holes on Barro Colorado Island, Panama. *Biotropica* 33: 110–120.

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