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RESEARCH

Patterns of woody plant epiphytism on tree ferns in New Zealand

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Abstract: Tree fern trunks provide establishment surfaces and habitat for a range of plant taxa including many understorey shrubs and canopy trees. The importance of these habitats for augmenting forest biodiversity and woody plant regeneration processes has been the subject of conjecture but has not been robustly assessed. We undertook a latitudinal study of the woody epiphytes and hemiepiphytes of two species of tree ferns (*Cyathea smithii*, *Dicksonia squarrosa*) at seven sites throughout New Zealand to determine (1) compositional variation with survey area, host identity, and tree fern size, and (2) the frequency of woody epiphyte and hemiepiphyte occurrence, in particular that of mature individuals. We recorded 3441 individuals of 61 species of woody epiphyte and hemiepiphyte on 700 tree ferns across the seven survey areas. All were facultative or accidental, with many species only ever recorded as seedlings. Epiphyte composition varied latitudinally in response to regional species pools; only two species occurred as woody epiphytes at every survey area: *Coprosma grandifolia* and *Schefflera digitata*. Five woody epiphyte species exhibited an apparent host preference to one of the two tree fern species surveyed, and trunk diameter and height were strong predictors of woody epiphyte and hemiepiphyte richness and diversity. Woody epiphytes and hemiepiphytes occurred on 59.7 ± 18.9% of tree ferns surveyed; yet mature epiphytes occurred on only 1.0 ± 0.6% of tree ferns. With the notable exception of some tree fern-*Weinmannia* communities, our data indicate that tree fern trunks are potentially not important as regeneration sites for most woody understorey and canopy species in New Zealand, instead acting more as sink habitats.

Keywords: tree fern, epiphyte, seedling establishment, forest ecology, hemiepiphyte, regeneration, *Weinmannia*

Introduction

Deep shade and mortality from disturbance in forest understories can be fundamental limitations on the regeneration of canopy trees and understorey shrubs (Coomes et al. 2005; Brock et al. 2018; Dawes & Burns 2020). Although viable seed continually arrives on the forest floor, and frequently germinates, deep litter, falling leaves, branches and fronds, and low light-levels prevent many seedlings from establishing (Gillman & Ogden 2005; Brock et al. 2018). Species that can establish on elevated surfaces such as fallen trunks, root boles, and tree fern trunks may stand a better chance of successful regeneration due to reduced disturbance and higher light-levels compared to the forest floor (Ogden 1971; Bellingham & Richardson 2006).

Tree ferns are a prominent feature of many southern hemisphere and tropical forests, in particular in the broadleaf-podocarp forests of New Zealand and forests of southeast Australia (Brock et al. 2016; Fedrigo et al. 2019). For some taxa, including members of the Cunoniaceae and Araliaceae, epiphytic regeneration is a key regeneration strategy to escape shade limitations of the forest floor (Putz & Holbrook 1986; Derroire et al. 2007), and can represent 60% of the stems in the canopy in some stands (Gaxiola et al. 2008).

New Zealand's tree fern epiphyte flora is rich; native vascular species recorded epiphytically on tree ferns include lycophytes, ferns, angiosperms, and even conifers (Pope 1926; Oliver 1930; Beveridge 1973; Veblen & Stewart 1980; Dawson 1988; Bellingham & Richardson 2006; Gaxiola et al. 2008; Brownsey & Perrie 2020). Specific communities of mosses and liverworts also establish on tree fern trunks (Beever 1984). Beever (1984) recorded 35 moss species on three tree fern species, with three moss species almost exclusively occurring on tree fern trunk habitats, and moss communities differing markedly among tree fern species.

Over thirty species of woody plants in New Zealand have been described as either obligate epiphytes, facultative epiphytes, or hemiepiphytes of tree ferns, particularly taxa from the Araliaceae (five spp.) and Cunoniaceae (four spp.), with many more observed as occasional seedlings (Pope 1926; Cooper 1956; Beveridge 1973; Veblen & Stewart 1980; Bellingham & Richardson 2006; Gaxiola et al. 2008). The most commonly described tree fern epiphytes in New Zealand are kāmahi *Weinmannia racemosa* and tōwai *W. sylvicola* (both Cunoniaceae) (Wardle & MacRae 1966).

Woody epiphytes of tree ferns have been described as important contributors to forest composition and structure, particularly in regard to whole stand regeneration of *Weinmannia* species (Beveridge 1973; Blaschke et al. 1992; Gaxiola et al. 2008). However, with the exception of tree fern-*Weinmannia* communities, the prevalence of woody plant epiphytism on understorey tree ferns has not been quantitatively assessed across New Zealand forests. Dawes

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and Burns (2020) described the importance of tree fern trunks as elevated establishment sites for small seeded woody species that would otherwise be limited by low light levels on the forest floor; however, the prevalence of these epiphytes across an understorey population of tree ferns was not reported.

Both qualitative and quantitative comparative studies on the abundance of epiphytes among different tree fern taxa have suggested that more epiphytes can be found on *Cyathea* spp. than *Dicksonia* spp. (Pope 1926; Dawson 1986; Ogden et al. 1986), but the opposite has been reported by Gaxiola et al. (2008). Further, Ogden et al. (1986) suggested that *W. sylvicola* preferentially establishes on *Dicksonia squarrosa*, but also recorded an apparent host preference of *Weinmannia* spp. for *Cyathea medullaris*. Ogden et al. (1986) also recorded an apparent lack of host preference in *Pseudopanax* spp. which occurred readily on all species of tree fern observed in the Kauaeranga Valley (Coromandel Peninsula). However, as all these studies were undertaken at a single forest location or within the same landscape, regional species pools will limit the epiphytic species available and hence any relationships observed between epiphytes and phorophytes. Burns (2010) highlighted the prevalence of obligate epiphytes in New Zealand forests; however, there are few obligate woody epiphytes in New Zealand. It seems likely therefore that in New Zealand most woody epiphytes of tree ferns are facultative or accidental (Burns 2010; Dawes & Burns 2020). Key to the ability of some woody plants to persist on tree fern trunks, however, is their capacity to eventually develop a root to the forest floor—the hemiepiphytes (Putz & Holbrook 1986; Zotz 2013).

Above a certain size threshold of conifer or angiosperm phorophytes, the richness and diversity of epiphyte communities increases proportional to the size (diameter at breast height; DBH) of the trunk (a proxy for age of establishment surface) (Taylor & Burns 2015). Tree ferns do not substantially increase their trunk diameter during their life (Brock et al. 2016), and a better proxy for their influence on the forest is height (Brock et al. 2020). The relationships between age of surface (height in tree ferns) and the richness and diversity of epiphytes on tree fern trunks are unknown.

In the tree fern order Cyatheales in New Zealand (excluding the creeping-stemmed *Loxsoma cunninghamii*), taxa produce rhizome structures that range in height and habit (erect / prostrate) (Brock et al. 2016). When the rhizome is erect as a trunk, the morphological traits of the trunk (fibrous adventitious root mantle, stipe bases, hairs, and / or scales) are consistent across all species of tree fern, with the exception of *Cyathea medullaris* and *Cyathea cunninghamii* in which the trunks consist largely of plate/frond scar material. Although *Cyathea medullaris* rarely supports woody epiphytes, where rainfall and humidity are high, individuals have been observed supporting species including *Aristotelia serrata*, *Melicytus ramiflorus*, *Brachyglottis repanda* and *Geniostoma ligustrifolium* (JB, pers. obs.). Furthermore, the prostrate nature of *Cyathea colensoi* and *Dicksonia lanata* subsp. *lantata*, the fully skirted nature of *Dicksonia fibrosa*, and the short stature, skirted form of *Dicksonia lanata* subsp. *hispida* reduces the establishment potential of woody epiphytes on these taxa. Those native New Zealand tree ferns that have both suitable surfaces and available surface area for woody epiphytes to regularly establish on are *Cyathea dealbata*, *Cyathea smithii*, and *Dicksonia squarrosa*.

In this study we focussed on *Cyathea smithii* and *Dicksonia squarrosa* because of their abundance and wide distribution along a latitudinal gradient from Northland to Rakiura (Lehmann et al. 2002; Brock et al. 2016). Although *C. smithii* has a skirt, and *D. squarrosa* an irregular skirt (a ring of dead fronds / stipes beneath the growing crown; Large & Braggins 2004), which arguably suppresses epiphyte establishment (Page & Brownsey 1986), both species support woody epiphytes (Ogden et al. 1986; Bellingham & Richardson 2006; Dawes & Burns 2020).

To date, no study has quantified the occurrence of woody epiphytism across tree ferns in New Zealand forests. Our study had the following aims:

(1) to compile observations of woody epiphyte and hemiepiphyte species on tree ferns in New Zealand through a literature review,

(2) to establish the frequency of occurrence of woody species epiphytism on tree ferns in native forest ecosystems, and the percentage of tree fern trunks that support non-ephemeral facultative, and accidental woody epiphytes,

(3) to quantify which native woody species are common epiphytes and hemiepiphytes of tree ferns, and the existence of any host preference of epiphyte/hemiepiphyte species, and,

(4) to establish whether woody epiphyte/hemiepiphyte communities respond to diameter, similar to forest canopy trees, or whether tree fern height is a more suitable predictor of woody plant establishment.

Methods

Review

A literature search was conducted using Scopus (www.scopus.com), ISI Web of Science (www.isiknowledge.com), and Google Scholar (https://scholar.google.com) databases. We used the search terms [“tree fern” OR “treefern” OR “tree-fern” AND “New Zealand” AND “epiphyt*”] with the search open to all subject areas. We compiled a list of vascular woody species recorded as having established on New Zealand tree ferns. Where not explicitly described as obligate, facultative, or accidental, as in Burns (2010), or as a hemiepiphyte (Zotz 2013), we used the description associated with each species found on tree ferns to assign habit (epiphyte or hemiepiphyte) and epiphyte type (obligate, facultative, or accidental).

Field Survey

We studied epiphytes from one species in each of the two tree fern families in New Zealand (Dicksoniaceae and Cyatheaceae): *Dicksonia squarrosa* and *Cyathea smithii*. The species were selected on the basis of their presence along a latitudinal gradient from Northland to Rakiura (Lehmann et al. 2002; Brock et al. 2016). Areas of forest supporting these species from Mataraua Plateau near Waipoua (35°36′51″S, 173°37′54″E) to Te Wharawhara (Ulva Island) (46°55′48″S, 168°07′22″E) were identified for survey, which comprised 12 sites across seven survey regions (Fig. 1). For each of the sites we extracted data on solar radiation, temperature, annual water deficit, and elevation from the LRIS portal (https://lris.scinfo.org.nz; Table 1). At each site, several 100 m transects were laid along access paths through the forest interior, and, following the point-centred quarter (PCQ) method at regular but < 20 m spacing (Mitchell 2015), 50 individuals of each species that were greater than two metres in height and that supported at least one vascular woody epiphyte were identified and sampled. Individuals < 2 m tall were not sampled as

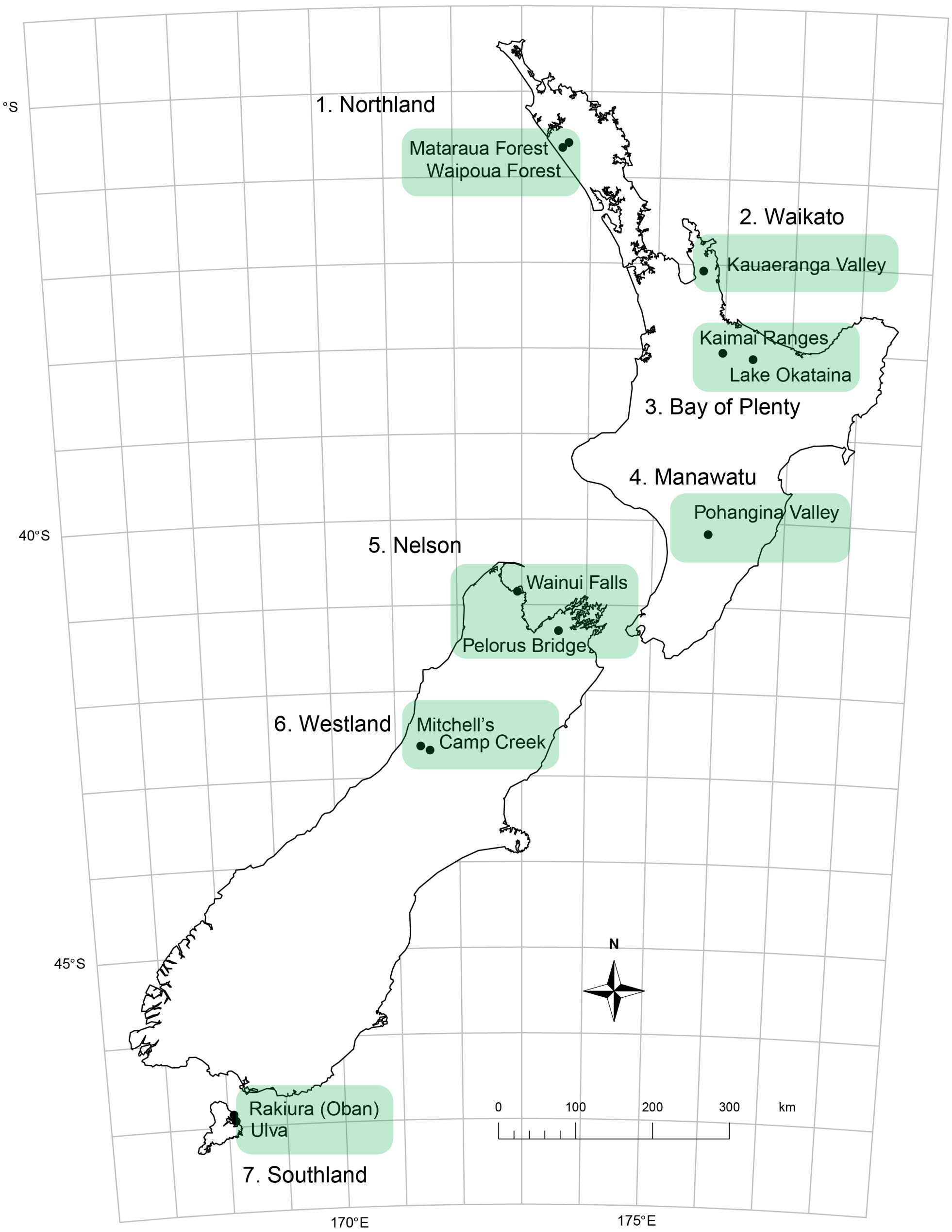

Figure 1. Locations of the seven survey regions (numbered) and 12 sites (highlighted) across New Zealand

Table 1. Modelled values of environmental variables (from LRIS Portal: https://lris.scinfo.org.nz) for each of the seven survey regions, and 12 survey sites.

Survey Regions	Survey Site	Mean annual solar radiation (MJ m^{-2} day^{-1})	Mean annual temperature (°C)	Mean annual water deficit (Index)	Elevation (m)
1. Northland	Mataraua Forest	146	12.1	0	602
	Waipoua Forest	146	12.8	0	432
2. Waikato	Kauaeranga Valley	149	13.6	13	171
3. Bay of Plenty	Kaimai Ranges	148	11.6	0	463
	Lake Okataina	151	11.8	0	401
4. Manawatu	Pohangina Valley	139	12.3	51	154
5. Nelson	Wainui Falls	151	12.5	0	50
	Pelorus Bridge	152	12.3	0	38
6. Westland	Mitchell's	130	10.6	0	226
	Camp Creek	130	11.0	0	150
7. Southland	Rakiura	119	9.5	0	85
	Ulva	119	9.6	0	67

woody epiphytes are rarely present on shorter-trunked tree ferns (JB, unpubl. data; Johansson 1974; Derroire et al. 2007; Dawes & Burns 2020). Height and DBH were recorded for every tree fern. Every woody epiphyte on each tree fern was identified to species (individuals that had only cotyledons were not recorded); epiphyte stem length and reproductive status (evidence of flowers, seed capsules etc.) were also recorded.

A secondary survey was undertaken at each site, again using the PCQ method, with the aim of establishing what proportion of the tree ferns in the forest supported woody epiphytes. Transects of up to 200 m were laid into the forest on a bearing generated by a random number generator. Points were established at 15 m spacing and the nearest tree fern of both species was identified in each quarter around the point (eight tree ferns per point). A visual assessment was made as to whether the trunk supported any identifiable woody seedlings.

Analysis

Review

The data were summarised in text and tabular form.

Epiphyte and hemiepiphyte occurrence

We compared the surface areas of the tree fern trunks (total, and exposed, i.e. not covered by skirt), and the densities of the various epiphyte habits (epiphytes or hemiepiphytes) and types (obligate, facultative, or accidental) using *t*-tests (corrected for pairwise family-wise error using Hochberg adjustments) between tree fern species. We also split species by whether they were ephemeral (only ever recorded as seedlings < 1.35 m tall); or persistent (saplings and mature plants observed). We compared richness and diversity (Shannon Wiener) of woody epiphytes and hemiepiphytes between tree fern host species using linear mixed effects models with survey region as a random effect.

We calculated percentages of those individuals that had developed beyond a seedling (stems > 1.35 m; Hurst & Allen 2007) as a percentage of all individuals of each species and repeated the exercise for those epiphytes that had developed to sexual maturity (flowers and/or fruit present).

Epiphyte and hemiepiphyte taxa and host preference

To establish whether woody epiphytes or hemiepiphytes of tree ferns had a host preference, we used a chi-squared test to analyse the frequency of occurrence on either *C. smithii* or *D. squarrosa*.

Epiphyte and hemiepiphyte response to size of host

We used linear mixed models with survey region and tree fern species as random effects, and DBH or tree fern trunk height as fixed effects to establish patterns between woody epiphyte and hemiepiphyte species diversity (Shannon Weiner diversity index), richness, and abundance and the size of the tree fern. All *p*-values were corrected to account for family-wise error rate using the Hochberg method.

Analyses were undertaken in R v4.0.2. in RStudio v1.0.143 (R Core Team 2015) and used the package lme4 v1.1-23 (Bates et al. 2015).

Results

Review

We identified 33 publications describing 45 different woody epiphyte or hemiepiphyte species of tree fern trunks from 21 families in New Zealand (see Appendix S1 in Supplementary Materials). The 45 species included two obligate epiphytes, seven facultative epiphytes, 15 facultative hemiepiphytes, 30 accidental epiphytes, and six species of accidental hemiepiphytes (species were described as being of more than one type).

Epiphyte and hemiepiphyte occurrence

The mean (± 1 SD) percentage of understorey tree fern trunks with woody epiphytes and hemiepiphytes present was 59.7 ± 18.9% across the seven regions (Table 2). The maximum percentage of tree fern trunks supporting woody epiphytes and hemiepiphytes recorded was 91.1% across the Westland survey region (Region 6), while the minimum was 28.4% in the Northland survey region (Region 1). There was no clear pattern of woody epiphytism on tree fern trunks in relation to climate (Table 1).

Only 4% of woody epiphytes recorded were greater than 1.35 m tall, i.e. a sapling or an adult tree. All woody epiphytes or hemiepiphytes recorded were facultative or accidental (infrequently recorded, predominantly on forest floor); 37 species were only ever recorded as a seedling and are identified as ephemeral epiphytes (Table 3).

We recorded 3441 woody epiphytes and hemiepiphytes on 700 tree ferns (350 of each species) across the seven regions (Fig. 1, Table 1). On the tree ferns that supported woody

Table 2. Woody species epiphytism on tree ferns in native forest in New Zealand.

Survey regions	Percentage of tree ferns supporting woody epiphytes			Number (% of total) of tree ferns that supporting woody epiphytes which also support:	
	Cyathea smithii	*Dicksonia squarrosa*	Both species	saplings or adults	reproductive epiphytes
1. Northland	28.0	28.8	28.4	15 (4.7)	5 (1.4)
2. Waikato	63.6	53.6	57.5	0 (0.0)	0 (0.0)
3. Bay of Plenty	60.6	60.0	60.3	3 (10.9)	3 (1.8)
4. Manawatu	50.8	55.1	53.0	3 (2.1)	3 (1.6)
5. Nelson	67.9	73.2	71.0	1 (5.7)	1 (0.7)
6. Westland	88.7	96.1	91.1	1 (20.0)	1 (0.9)
7. Southland	51.3	62.5	56.9	1 (5.7)	1 (0.6)
Mean ± SD	58.7 ± 18.6	61.3 ± 20.5	59.7 ± 18.9	3.4 ± 5.2 (7.0 ± 6.7)	2.0 ± 1.7 (1.0 ± 0.6)

Table 3. Details of facultative / accidental epiphytes and hemiepiphytes, and ephemeral epiphytes of *Cyathea smithii* and *Dicksonia squarrosa* recorded across all survey regions. Reproductively mature epiphytes and hemiepiphytes are in grey. Survey regions north to south: 1 = Northland, 2 = Waikato, 3 = Bay of Plenty, 4 = Manawatu, 5 = Nelson, 6 = Westland, 7 = Southland. Species names follow Ngā Tipu o Aotearoa (https://ltl.lincoln.ac.nz/nga-tipu-o-aotearoa-new-zealand-plants/).

Epiphyte species	Family	Persistence	No. of occurrences	Max height per species (cm)	Survey regions						
					1	2	3	4	5	6	7
Facultative hemiepiphytes (9 mature spp., 1 sapling spp.)											
Ackama rosifolia	Cunoniaceae	persistent	331	650	X						
Griselinia littoralis	Griseliniaceae	persistent	30	140						X	X
Griselinia lucida	Griseliniaceae	persistent	8	500	X						
Melicytus ramiflorus	Violaceae	persistent	333	400		X	X	X	X	X	
Melicytus macrophyllus	Violaceae	persistent	36	330	X						
Pseudopanax arboreus	Araliaceae	persistent	76	560		X	X	X	X		
Raukaua edgerleyi	Araliaceae	persistent	37	620	X				X	X	X
Schefflera digitata	Araliaceae	persistent	149	420	X	X	X	X	X	X	X
Weinmannia racemosa	Cunoniaceae	persistent	1179	560			X		X	X	X
Weinmannia sylvicola	Cunoniaceae	persistent	229	1100	X	X					
Accidental epiphytes (5 mature spp., 9 sapling spp., 37 ephemeral spp.)											
Alectryon excelsus	Sapindaceae	ephemeral	1	8				X			
Alseuosmia macrophylla	Alseuosmiaceae	persistent	8	205	X	X	X				
Aristotelia serrata	Elaeocarpaceae	ephemeral	87	90			X	X		X	X
Beilschmiedia tawa	Lauraceae	ephemeral	17	60			X	X			
Brachyglottis kirkii var. *kirkii*	Asteraceae	ephemeral	3	110	X				X		
Brachyglottis myrianthos	Asteraceae	ephemeral	2	30		X					
Brachyglottis repanda	Asteraceae	persistent	29	390	X			X			
Brachyglottis rotundifolia	Asteraceae	persistent	1	135							X
Carpodetus serratus	Rousseaceae	ephemeral	49	50		X	X			X	X
Coprosma areolata	Rubiaceae	ephemeral	19	65		X			X		X
Coprosma foetidissima	Rubiaceae	persistent	27	170							X
Coprosma grandifolia	Rubiaceae	persistent	73	350	X	X	X	X	X	X	X
Coprosma lucida	Rubiaceae	persistent	28	350	X	X	X			X	X
Coprosma robusta	Rubiaceae	ephemeral	5	45		X					
Coprosma tenuifolium	Rubiaceae	persistent	1	125						X	
Dacrycarpus dacrydioides	Podocarpaceae	ephemeral	7	15			X	X	X		
Dacrydium cupressinum	Podocarpaceae	ephemeral	5	97					X		X
Dracophyllum latifolium	Ericaceae	persistent	3	240	X						
Dracophyllum longifolium	Ericaceae	ephemeral	1	20							X
Elaeocarpus dentatus	Elaeocarpaceae	persistent	3	167	X	X					
Fuchsia excorticata	Onagraceae	ephemeral	6	20							X
Geniostoma ligustrifolium	Loganiaceae	persistent	144	270	X	X	X	X			
Hedycarya arborea	Monimiaceae	ephemeral	13	36	X	X		X	X	X	
Ixerba brexioides	Strasburgeriaceae	ephemeral	1	10	X		X				
Knightia excelsa	Proteaceae	ephemeral	17	14	X	X	X	X			
Kunzea ericoides	Myrtaceae	ephemeral	2	25					X		
Kunzea robusta	Myrtaceae	ephemeral	16	25		X					
Laurelia novae-zelandiae	Atherospermataceae	ephemeral	9	15	X		X				
Leptospermum scoparium	Myrtaceae	ephemeral	1	15							X
Leucopogon fasciculatus	Ericaceae	ephemeral	2	50	X	X					
Metrosideros robusta	Myrtaceae	ephemeral	2	30		X					
Metrosideros umbellata	Myrtaceae	ephemeral	17	62					X		X
Myrsine australis	Primulaceae	ephemeral	98	110		X	X			X	X
Myrsine salicina	Primulaceae	ephemeral	1	12		X					
Olearia rani	Asteraceae	persistent	14	310		X	X		X		
Pectinopitys ferruginea	Podocarpaceae	ephemeral	8	70	X					X	X
Pennantia corymbosa	Pennantiaceae	ephemeral	2	18					X		X
Phyllocladus trichomanoides	Podocarpaceae	ephemeral	13	100		X					

Table 3. Continued.

Epiphyte species	Family	Persistence	No. of occurrences	Max height per species (cm)	Survey regions 1	2	3	4	5	6	7
Piper excelsum	Piperaceae	ephemeral	4	25				X			
Pittosporum huttonianum	Pittosporaceae	ephemeral	1	26		X					
Pittosporum tenuifolium	Pittosporaceae	ephemeral	3	70							X
Podocarpus totara	Podocarpaceae	persistent	4	360	X			X			X
Prumnopitys taxifolia	Podocarpaceae	ephemeral	2	11					X		
Pseudopanax crassifolius	Araliaceae	persistent	41	200	X	X		X	X		X
Pseudowintera colorata	Winteraceae	ephemeral	4	45						X	
Quintinia serrata	Paracryphiaceae	ephemeral	34	85						X	
Rhopalostylis sapida	Arecaeae	ephemeral	2	5	X						
Rubus cissoides	Rosaceae	ephemeral	1	5						X	
Streblus heterophyllus	Moraceae	persistent	1	340				X			
Syzygium maire	Myrtaceae	ephemeral	2	17	X						
Veronica spp.	Plantaginaceae	ephemeral	1	8						X	

Table 4. Comparison of available surface area and epiphyte densities (for those tree ferns that supported at least one woody epiphyte) between *C. smithii* and *D. squarrosa*. All *P*-values have been corrected for family-wise error using the Hochberg method.

	Cyathea smithii	*Dicksonia squarrosa*	t	df	*P*-value
Establishment area (m^2 tree fern^{-1}) $\bar{x}$ ± SD (n)					
Mean surface area of trunk	2.42 ± 1.38 (350)	1.56 ± 0.91 (350)	9.6882	605.85	**< 0.001**
Mean surface area of trunk not covered by skirt	1.80 ± 1.17 (350)	1.46 ± 0.93 (350)	4.3772	671.58	**< 0.001**
Density measures (m^{-2} tree fern^{-1}) $\bar{x}$ ± SD (n)					
Total epiphyte and hemi-epiphyte density	2.5 ± 3.4 (1745)	3.5 ± 3.5 (1658)	−1.2876	698.93	0.1983
Facultative hemi-epiphyte density	1.56 ± 1.95 (285)	2.60 ± 3.26 (299)	−5.1682	572.8	**< 0.001**
Accidental epiphyte density	0.33 ± 0.70 (118)	0.29 ± 0.69 (590)	0.75851	698.87	0.4484

epiphytes and/or hemiepiphytes, mean total epiphyte and hemiepiphyte density across all sites was 3.0 ± 3.5 m^{-2} trunk surface area with a maximum recorded density of 37.1 m^{-2}. The maximum density was observed on a *Cyathea smithii* at the Camp Creek site in the Westland survey region (3.6 m tall; 12.4 cm DBH; 52 woody epiphyte and hemiepiphyte individuals of two species). Although the tree fern species varied significantly ($t = 9.6882$, $P < 0.001$) in available establishment surface area (area of trunk not obscured by skirt) for epiphytes (*D. squarrosa* = 1.5 m^2 tree fern^{-1}, *C. smithii* = 1.8 m^2 tree fern^{-1}), no difference in epiphyte and hemiepiphyte density was observed ($t = -1.288$, $P = 0.198$; Table 4). Further, there were no significant differences in the densities recorded of accidental epiphytes between the two tree fern taxa (Table 4); however, *D. squarrosa* supported significantly higher densities (c. 1 m^{-2} more than *C. smithii*) of facultative hemiepiphytes ($t = -5.1682$, $P < 0.001$; Table 4), although abundance of facultative hemi-epiphytes per trunk were similar (*D. squarrosa* = 3.67 ± 4.36; *C. smithii* = 3.23 ± 4.26).

Mean woody epiphyte and hemiepiphyte richness (on tree ferns that supported woody epiphytes and hemiepiphytes) was 2.0 ± 1.1 species tree fern^{-1} with a maximum recorded richness of eight woody epiphyte and hemiepiphyte species on a single trunk. *Cyathea smithii* hosted a greater ($F_{1–693}$ = 10.89, P = 0.001) woody epiphyte and hemiepiphyte richness on average (2.1 ± 1.2, compared to *D. squarrosa* 1.9 ± 1.0 species tree fern^{-1}). As a consequence, diversity of woody epiphytes and hemiepiphytes was also higher ($F_{1–693}$ = 4202.16, $P < 0.001$) on *C. smithii* (0.54 ± 0.48) than *D. squarrosa* (0.42 ± 0.44).

Only 3.9% (n = 133) of woody epiphytes and hemiepiphytes were recorded as saplings (> 1.35 m) or larger, and 0.6% (n = 19) of woody epiphytes and hemi-epiphytes were recorded as reproductive (Appendix S2). Across all sites, an average of 2.3 ± 1.7 woody epiphyte and hemiepiphyte species per site were identified as having developed to sexual maturity. Of 700 tree ferns surveyed, only 95 (14%) supported woody epiphytes and hemiepiphytes that were saplings or adults, and 14 (2%) supported woody epiphytes and hemiepiphytes that were reproductive.

Epiphyte and hemiepiphyte taxa and host preference

In total 61 species from 29 families were recorded on the trunks of *C. smithii* (55 species) and *D. squarrosa* (50 species) (Table 3). Only 24 species across 12 families were recorded as saplings or adults, and only 14 species from eleven families were recorded as reproductive (Table 3). Nine of the reproductive species (Araliaceae: *Pseudopanax arboreus*, *Raukaua edgerleyi*, *Schefflera digitata*; Cunoniaceae: *Ackama rosifolia*, *Weinmannia racemosa*, *Weinmannia sylvicola*; Griseliniaceae: *Griselinia lucida*; Violaceae: *Melicytus ramiflorus*, *Melicytus macrophyllus*) were recorded as developing roots that reached the forest floor (hemiepiphytes). The remaining five species (four families) of reproductive woody plant were recorded as having truly epiphytic habit (though facultative) on tree fern trunks: *Alseuosmia macrophylla* (Alseuosmiaceae), *Brachyglottis repanda* (Asteraceae), *Coprosma grandifolia* (Rubiaceae), *Coprosma lucida* (Rubiaceae), and *Geniostoma ligustrifolium* (Loganiaceae).

Species that represented more than 5% of the total abundance of woody epiphytes and hemiepiphytes recorded were *W. racemosa* (n = 1179, 34% of total epiphytes recorded), *M. ramiflorus* (Violaceae, 333, 10%), *W. sylvicola* (229, 7%), *S. digitata* (149, 5%), and *A. rosifolia* (331, 10%).

Of 61 species, only two were recorded as an epiphyte at every area: *C. grandifolia* (n = 126, 3.7%) and *S. digitata*. Although *Weinmannia* spp. represent 41% of the total recorded epiphytes and hemiepiphytes, neither species was recorded at the Pohangina River site in the Manawatu (Region 4), the site with the highest mean annual water deficit (Table 1).

With regard to host preference of facultative woody epiphytes and hemiepiphytes, five species were recorded more frequently ($X^2_{(12, N = 249)} = 228.9$, $p < 0.0001$) on one or other host tree fern species: *W. racemosa*, *S. digitata*, and *C. grandifolia* occurred more frequently on *C. smithii*, whilst *A. rosifolia* and *W. sylvicola* occurred more frequently on *D. squarrosa*. A number of facultative epiphytes identified in the literature review were not recorded during our surveys (*Ackama nubicola*, *Dracophyllum arboreum*, *Metrosideros bartlettii* and *Myrsine chathamica*); we also did not record two obligate epiphytes identified in our review (*Pittosporum cornifolium* and *Pittosporum kirkii*) (Table 3, Appendix S1). Further, we recorded three species not previously described as epiphytes of tree ferns: *Alseuosmia macrophylla*, *Coprosma lucida*, and *Melicytus macrophyllus* (Table 3, Appendix S1).

Epiphyte response to size of host

Tree fern height and DBH were predictors of woody epiphyte and hemiepiphyte richness (height: t = 3.007, P = 0.0003; DBH: t = 2.646, P = 0.0112) and diversity (height: t = 5.678, P < 0.0001; DBH: t = 6.49, P < 0.0001) regardless of tree fern species identity and survey location (Appendix S3). Woody epiphyte and hemiepiphyte abundance was not correlated to either height or DBH (Appendix S3).

Discussion

This is the first study to quantify woody plant epiphytism on tree ferns across New Zealand, and to provide an indication of the frequency of occurrence of successful hemi- and accidental epiphytism by native species on tree fern trunks. We highlight five species of accidental epiphyte and nine species of hemiepiphyte that we commonly found on tree ferns throughout New Zealand native forests that developed to reproductive maturity. However, a rich array of other shrubs, small trees and canopy tree species established on tree ferns.

The distinct differences in the frequency of woody epiphytism of tree fern trunks across the country likely reflect variation in a combination of environmental conditions, and competition. The high frequency of woody epiphyte occurrence in the Westland survey region (Region 6) is likely a response to the high annual levels of rainfall experienced in Westland (Caloiero 2014). In contrast, the surveyed tree ferns in Northland (Region 1) were significantly less frequently colonised by woody epiphytes and hemiepiphytes than in all other areas. The tree ferns at the Northland survey region, particularly those in the Mataraua Forest site were frequently densely covered in filmy ferns (Hymenophyllaceae), moss, and liverwort species as this area is cloud forest (Singers & Rogers 2014). Although no quantitative data on trunk cover by ferns and mosses were collected during surveys, such cover in Northland appeared significantly greater than in Westland. Bryophytes and filmy ferns can have a negative allelopathic effect on the germination of woody species (Froude 1980; Michel et al. 2011), likely reducing the frequency of epiphytic establishment in the northern forests. The dense covering of bryophytes and filmy ferns forms a physical barrier that may prevent seeds from lodging in the root mantle and stipe bases. Further studies are needed on the potential for competitive exclusion of woody plants by filmy ferns and bryophytes in areas of high humidity, as compared to areas of high rainfall (cloud forest vs rainforest).

Although the richness and diversity of woody epiphyte and hemiepiphyte species were slightly higher on *C. smithii* than *D. squarrosa*, there was no difference in the densities of woody epiphytes establishing on the two tree fern taxa in our study. The consistency in epiphyte density between these tree fern taxa varies from the differences observed among species in Réunion and Australia (Ashton 2000; Rivière et al. 2008). Qualitative assessments of tree fern epiphytism, including our observations during the field survey, indicated a higher density of woody epiphytes on *Cyathea* than *Dicksonia* (e.g. Pope 1926; Dawson 1986; Ogden et al. 1986). Correction for stem surface area, however, removes any difference between taxa. The maximum density of woody epiphytes and hemiepiphytes that we recorded was 37 m^{-2}; this is higher than the 5.2 epiphytes m^{-2} reported for *Cyathea divergens* in a Mexican tropical cloud forest (Mehltreter et al. 2005) even though Mehltreter et al. (2005) included ferns as well as woody epiphytes. Of interest is the higher density of facultative hemiepiphyte species on *D. squarrosa* than on *C. smithii*; however, given that *D. squarrosa* provides less surface area than *C. smithii* the actual numbers of facultative hemiepiphytes per trunk do not differ between tree fern taxa.

Of the woody epiphyte and hemiepiphyte species identified in our literature review but not recorded during our field survey, these were likely unrecorded due to rarity (*Ackama nubicola*, *Metrosideros bartlettii*, and *Pittosporum kirkii*; de Lange et al. 2018) or as they are endemic to the Chatham Islands (*Myrsine chathamica*, *Dracophyllum arboreum*). *Pittosporum cornifolium* was most likely not recorded as few of the tree ferns we surveyed supported *Astelia* species – a key host of *P. cornifolium* occurring in mature forest (Bellvé 2018; Taranaki Regional Council 2020). We also recorded a species that was not identified in the published literature as a tree fern epiphyte: *A. macrophylla* was recorded at a number of survey areas as a low-trunk epiphyte of tree fern trunks. Given that epiphytes of this species always establish at the base of the tree fern it is likely that at least some of the roots of adult individuals reach the soil rendering this species a facultative hemiepiphyte. However, it was not possible to confirm this without damaging the roots around the base of the tree fern.

Outside areas that support successional forest communities in which *Weinmannia* species preferentially establish as epiphytes on tree ferns (Beveridge 1973; Blaschke et al. 1992; Gaxiola et al. 2008), as few as 1 in 175 tree ferns support mature woody epiphytes. Excluding tree fern–*Weinmannia* spp. communities (Wardle & MacRae 1966), and assuming a mean understorey tree fern density of 640 ± 653 tree ferns ha^{-1} (JB, unpubl. data) in northern New Zealand forests, the potential range in densities of mature woody tree fern epiphytes and hemiepiphytes is between 3.8 ± 3.9 and 11.5 ± 11.6 ha^{-1}. Spread across a possible 2.1 species of successfully maturing epiphytes (mean across all New Zealand) reduces this to between 1 and 5 individuals of any woody species per hectare capable of establishing epiphytically. On this basis, our data indicate that tree fern trunks are potentially of limited importance as regeneration sites for most woody understorey and canopy species in New Zealand, acting more as sink habitats. Long-term studies looking at the demography (recruitment, growth, mortality) of populations of woody seedlings establishing on tree fern trunks over time are needed to answer this question.

Interestingly, there may be a host preference (based on frequency of occurrence data) of some woody epiphytes, with two species (*Ackama rosifolia*, *Weinmannia sylvicola*) occurring more frequently on *Dicksonia squarrosa*, and three species (*W. racemosa*, *Schefflera digitata*, and *Coprosma grandifolia*) occurring more frequently on *Cyathea smithii*. Host preference of some New Zealand epiphytes has previously been observed in *Hymenophyllum malingii* (never on tree ferns) and *Phlegmariurus* species. *Phlegmariurus billardierei* never occurs on tree ferns, whereas *P. varius* often does (Brownsey & Perrie 2020). However, there are no published data showing discrimination of vascular epiphytes across tree fern taxa. While we cannot explain host preferences of wind dispersed species (*A. rosifolia*, *Weinmannia* spp.), there are several potential drivers of this pattern in endozoochorous epiphytes: (1) differing microbial and fungal composition of the trunks between the tree fern taxa driving biotic competition in the epiphyte regeneration niche (Orlovich et al. 2013), (2) trunk surface conditions are more suitable for establishment of fleshy-fruited species on *C. smithii*, and (3) birds carrying seed are drawn to *C. smithii* more than *D. squarrosa*, perhaps for foraging purposes (e.g. for scales of *Cyathea* for nesting materials; Ramsay 1865; Powlesland et al. 2000; Low 2004). However, tīeke *Philesturnus carunculatus* have been observed foraging on *D. squarrosa* up to twice the length of time than on *C. smithii* on Rakiura (Michel et al. 2010). The outcome of our study counters the comments of Dawson (1986) who described the apparent preferred host of *W. racemosa* as *D. squarrosa*. Further studies on establishment surface conditions and germination rates should be undertaken to identify potential drivers of the apparent host-preferences.

Richness and diversity of woody epiphytes increased with height and DBH of tree ferns; the strongest predictor of these indices was height. In terms of potential to support woody epiphytes, tree ferns have a similar relationship to that between trees and their epiphytic communities in terms of DBH (Burns & Dawson 2005; Taylor & Burns 2015), but height is a more informative parameter (as Brock et al. 2020). This finding is of relevance to forest modellers who should consider including height increment as a tree fern growth parameter in forest models, particularly where epiphytic establishment is a key consideration (e.g. *Weinmannia* spp. establishment processes) to ensure a more effective representation of the relationships between woody epiphyte and tree fern.

Although this study did not focus on all native tree fern species capable of supporting woody epiphytes, we characterised epiphytes on the two most widely distributed, and common species (Brock et al. 2016). It is highly probable that we have not captured all ephemeral woody epiphytes that might germinate on tree ferns. The authors have incidentally observed the most unlikely of ephemeral epiphytes, kauri *Agathis australis*, as a sapling (> 1.35 m, DBH c. 1 cm) on a *Cyathea medullaris* trunk in the Waitākere Ranges west of Auckland, and a *D. squarrosa* growing from the trunk of a *Cyathea dealbata* also in the Waitākere Ranges (JB and BB, unpubl. data). As most of the fieldwork for this study was undertaken in forest parks and reserves, away from more disturbed areas of the landscape, no non-native woody species were recorded. However, a mature European gorse *Ulex europaeus* was observed on *C. smithii* near Hokitika, and a mature Himalayan honeysuckle *Leycesteria formosa* on *D. squarrosa* near Rotorua (JB, unpubl. data). It is probable that other non-native woody species will also establish in this manner in urban areas or more intensively managed landscapes, and where propagule rain is sufficient.

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Author contributions

JB and BB conceived the project idea, survey work was coordinated and undertaken by JB & BB. Analysis and writing were undertaken by JB and reviewed by BB.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Woody epiphytes and hemiepiphytes of tree fern trunks as identified by a literature review.

Appendix S2. Percentage occurrence of saplings (> 135 cm tall, but not reproductive) and reproductive individual woody epiphytes by species and survey area.

Appendix S3. Model parameters for linear mixed models of woody epiphyte and hemiepiphyte diversity, richness, and abundance using DBH and tree fern height as fixed effects, with tree fern species and survey area as random effects.

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