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Tree fern ecology in New Zealand: A model for southern temperate rainforests

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ABSTRACT

Tree ferns are a ubiquitous and often locally dominant element of wet southern temperate rainforests across Australasia, southern Africa and in regions adjacent to the tropics in South America. Published data on the ecology of tree ferns throughout these forest ecosystems is piecemeal, with the most comprehensive literature describing the ecology of tree ferns coming from New Zealand. Therefore using New Zealand forests as a model system, we review the ecology and importance of tree ferns for forest structure and composition. Most studies of the ecology and function of forest species in New Zealand have focussed on spermatophytes. Even though tree ferns (Cyatheaceae, Dicksoniaceae) can represent more than 50% of basal area and more than 20% of forest biomass they have been largely overlooked and quantitative information on their contribution to forest structure and function is relatively scarce. Here for the first time we synthesise information on NZ's indigenous tree ferns published over the last 100 years and present new data on their ecology and potential ecosystem influences. Irradiance and nutrient (N, P) levels constrain development of tree fern gametophytes, with P limitation potentially influencing sporophyte production. Tree ferns establish during temporary removal of forest canopies across various spatio-temporal scales including after local disturbances, wind-throw openings of the canopy, and landslides. Members of the Cyatheaceae exhibit spatial differentiation along temperature and solar radiation gradients; the Dicksoniaceae species differentiate most strongly on their frost tolerance. Frequency/abundance of all nine understory tree fern species indigenous to New Zealand increases with total soil phosphorus, with some niche differentiation among species along a broader nutrient gradient. Tree ferns are prominent in early and mid-successional forest communities where they may persist for more than 250 years. Individually, and as a group, tree-ferns impact nutrient cycling, organic matter accumulation and ground-level irradiance, often shading out tree seedlings. Tree ferns also have long-term physical impacts on the regeneration niche of associated species, with epiphytism on tree fern trunks providing alternative establishment surfaces for many species. Domination of nutrient resources by tree ferns early in succession is likely a key factor influencing community establishment. We conclude with key recommendations for future research on fundamental unknown elements of the ecology and synecology of tree ferns including greater determination of their ecophysiology and influence on forest community assemblages.

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1. Introduction

Tree ferns are a well-established clade within the leptosporangiate ferns dominating the order Cyatheales (Korall et al., 2006; Christenhusz et al., 2011). Many of these ferns have escaped the confines of the forest understorey (see Section 2) by evolving trunk-like structures (caudex) comprising a columnar base of adventitious roots, a root mantle, and an upper trunk of dead stipes (Roberts et al., 2005; McGhee, 2011). Originating from different organs, the trunks of tree ferns are also distinguished from the woody trunks of angiosperms and conifers by having a pith core surrounded by a starch-filled cortex, with the axial strength of the trunk derived from crescent-shaped vascular bundles surrounded by lignin impregnated sclerenchyma (Large and Braggins, 2004). This successful life-form, which arose in the early Carboniferous (DiMichele and Phillips, 2002), has enabled tree ferns to diversify across the tropics, sub-tropics and both the northern and southern temperate zones, with the greatest species richness of the (approximately) 650 taxa in the Cyatheaceae and Dicksoniaceae (Conant et al., 1995; Churchill et al., 1998) in the tropical region (Large and Braggins, 2004; Arcand et al., 2008; Korall and Pryer, 2014). The Cyatheaceae is the family with the greatest latitudinal extent (23°N to 50°S latitude).

The forest ecosystems of New Zealand are relatively well understood (Enright and Hill, 1995; Veblen et al., 1996; Wiser et al., 2011; Allen et al., 2013), and tree ferns are a dominant component of many vegetation communities (Wardle, 1991) across the latitudinal range of the three main islands of this country (McGlone et al., 2010), more so than in most other regions. We therefore examine tree ferns in New Zealand as a model system to understand the influence of tree ferns on forest assemblages; with literature from outside New Zealand and the southern temperate biome incorporated, where relevant, to generalise our arguments. The historic lack of natural fire in New Zealand's ecosystems (Perry et al., 2014) potentially confounds comparisons with Australia and South Africa; we provide a comparison of the response of tree ferns in New Zealand's contemporary ecosystems (where anthropic fire is now common) to that of tree ferns in other regions with higher natural fire activity.

The indigenous temperate evergreen rainforests of New Zealand (see Fig. 1 for illustration of main islands and sites referred to herein) include a range of mixed angiosperm (Cunoniaceae, Lauraceae, Myrtaceae, Nothofagaceae)-conifer (Podocarpaceae, Araucariaceae, Cupressaceae) communities (Ogden, 1985; Wiser et al., 2011) that have a high proportion (c. 82%) of endemic vascular plant species (McGlone et al., 2001). This level of endemism is mirrored in the tree ferns, with 80% (8 of 10) of the taxa endemic (Allan, 1961; Large and Braggins, 2004). Tree ferns are present throughout modern New Zealand forest ecosystems, from sea level to 1500 m above sea level and from 34°S to 50°S. Only one introduced species, *Cyathea cooperi*, an Australian species first recorded growing outside of cultivation in New Zealand in 1993 (Gardner, 1994), occurs, and it is currently limited to the Auckland region (Heenan et al., 1998).

New Zealand's modern tree fern assemblage has at least a 35 - 30 million year spore and macrofossil record (Brownsey, 2001; Perrie and Brownsey, 2007; Homes et al., 2015), and probably dates back to the Cretaceous at the generic level (Cieraad and Lee, 2006). Fossils of Dicksoniaceae and Cyatheaceae are recorded from the Triassic and early Cretaceous, respectively, with the genera *Dicksonia* and *Cyathea* first appearing in New Zealand's spore record during the Cretaceous period, around 85 – 66 mya (Cieraad and Lee, 2006). The earliest records of spore-types of modern species from New Zealand are from the Paleocene (56–66 mya) for *Cyathea dealbata* and *Dicksonia squarrosa*, Eocene (33.9–56 mya) for *Cyathea smithii* and the Miocene (5.5–23 mya) for *Cyathea colensoi*, *Cyathea medullaris*, *Dicksonia lanata*, and *Dicksonia fibrosa*. These tree fern species have consequently been continually present in New Zealand forest assemblages since the Paleocene (Lee et al., 2012) and are, therefore, an ancient Gondwanan component of New Zealand's indigenous forest ecosystems.

Since human settlement of New Zealand, around 1280 CE (Wilmshurst et al., 2008), forest clearance disturbances through burning and logging have reduced the forest cover from 85% to c. 23% and significantly transformed the landscape (McGlone, 1989; Perry et al., 2014). In addition the introduction of invasive mammalian species has influenced the composition and structure of New Zealand forests (Atkinson, 2006). Tree fern species effectively colonise recently disturbed sites such as those arising from land clearance. This pioneer role was demonstrated early in New Zealand's European history when Captain Cook cleared an area of land at Ships Cove, Marlborough, in 1770 attempting to establish a wheat crop. The trial failed and a grove of tree ferns (species unrecorded) established displacing the wheat (Pope, 1924).

Tree ferns do not play a significant role in modern forestry and silviculture in New Zealand or elsewhere; they are, however, collected for horticultural use in New Zealand (Veale, 1986), and are harvested in vast numbers for export from Tasmania and Victoria to service an international ornamental market. More than 140,000 *Dicksonia* were imported into the United Kingdom between 1995 and 2000, and recently attempts have been made to cultivate *Dicksonia* in Australia to provide a sustainable source of these desirable plants (Unwin and Hunt, 1997; Lawson, 2002; Vulcz et al., 2002).

Few (13) publications specifically focus on tree ferns in New Zealand forest communities, although numerous studies exist that

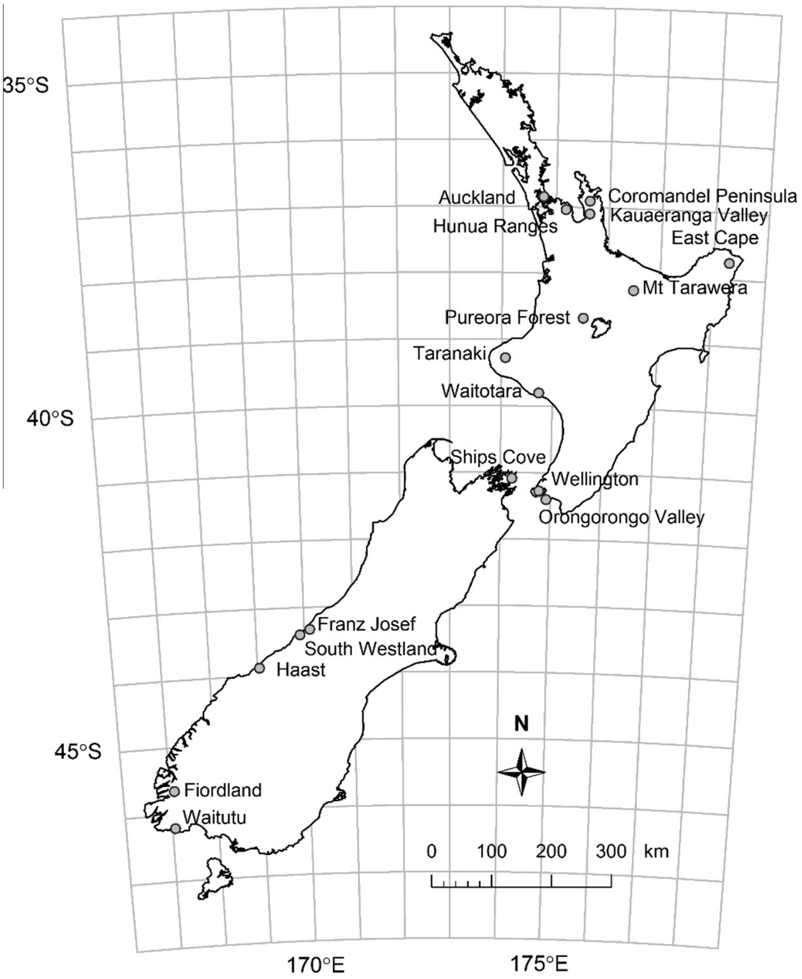

Fig. 1. The main islands of New Zealand including the place names of locations mentioned in the text.

contain other insightful information. This review provides an overview of tree fern ecology in New Zealand, with a focus on their role in forest community dynamics, as a model for southern temperate rainforests. We identify the key specific gaps in our current knowledge of tree fern ecology, highlight the significant general gap in the knowledge of tree fern ecology across the biome, and suggest how future research might fill these.

2. What is a tree fern?

The term 'tree fern' includes, but is not limited to, ferns with trunk-like structures in the order Cyatheales (Large and Braggins, 2004; Korall et al., 2006; Smith et al., 2006). Taxa of the eight families that comprise this order are highly varied in habit including the inconsistent presence of a distinctive trunked form (Kubitzki, 1990; Korall et al., 2006) characteristic of the Cyatheaceae and Dicksoniaceae. Confusingly, the expression of a trunk is not limited to the Cyatheales, being rarely found in other fern families (e.g. Blechnaceae) (Korall et al., 2006). Two main morphological synapomorphies have been identified for tree fern taxa: the presence of pneumathodes (pneumatophores or aerophores) and radial shoot symmetry, the latter is considered the predominant character although it is homoplastic in the Loxomataceae and Metaxyaceae (Pryer et al., 1995; Wolf et al., 1999; Korall et al., 2006).

The trunk growth forms in tree ferns are highly variable and include creeping, ascendant and erect habits (Ward and Cranwell, 1993; Large and Braggins, 2004; Korall et al., 2006); tree ferns with erect forms, i.e. producing a stem or trunk-like structure are described as arborescent, and are the subject of this review. In New Zealand there are 10 native species of arborescent tree ferns (Table 1); this excludes one sub-species of the Dicksoniaceae, the entirely prostrate *D. lanata* subsp. *lanata* (Brownsey and Perrie, 2014).

Phylogenetic analysis (Korall and Pryer, 2014) suggests that the Cyatheaceae could be split into four lineages at the genus level: *Cyathea*, *Sphaeropteris*, *Alsophila*, *Gymnosphaeris*. In this revised classification the New Zealand species would be placed in *Alsophila* with the exception of *C. medullaris*, which would be the sole New Zealand representative of *Sphaeropteris*. However, this revision has not been adopted and so the nomenclature in this review follows the Ngā Tipu Aotearoa – New Zealand Plants database (Landcare Research, 2014), which places all of the New Zealand members of the Cyatheaceae in the genus *Cyathea*.

3. Autecology of New Zealand's tree ferns

3.1. Spore dispersal and viability

Tree fern sporophytes produce abundant small spores that are readily wind dispersed, with spore sizes for the New Zealand *Cyathea* species range from 39 to 49 μm (Braggins and Large, 1990). Conant (1978) estimated that a mature *Cyathea arborea* could produce 492,800 spores annually. Tree ferns are therefore capable of colonising most habitats and are unlikely to be dispersal

Table 1
Native arborescent tree fern species of New Zealand with recorded trunk heights and frond lengths (Allan, 1961; Large and Braggins, 2004; NZPCN, 2013); all Māori and pākehā (European) names encountered during the review are listed for each species with nomenclature following the Ngā Tipu Aotearoa – New Zealand Plants database (Landcare Research, 2014). New Zealand tree ferns, *C. medullaris* and *C. cunninghamii* are among the tallest tree ferns globally (Large and Braggins, 2004); the former has been reliably measured at 19.6 ± 0.6 m in the Kauaeranga Valley, Coromandel (Brock, unpublished data).

Species	Common name	Max recorded height (m)	Max frond length (m)
Cyatheaceae – scaly tree ferns			
Cyathea colensoi	Grove-fern, stemless, rough, mountain or creeping tree fern	⩽1	1.5
C. cunninghamii	Ponga, pūnui, gully or slender tree fern	20	3
C. dealbata	Ponga, punga, kaponga or silver fern	10	4
C. kermadecensis	Kermadec tree fern	20	4
C. medullaris	Mamaku, kōrau, katātā, pītau, black mamaku or black tree fern	20	6
C. milnei	Milne's tree fern	8	4
C. smithii	Kātote, whē, neineikura, ponga, soft or Smith's tree fern	8	2.5
Dicksoniaceae – hairy tree ferns			
Dicksonia fibrosa	Kuranui-pākā, kurīpākā, pūnui, tūkirunga, wekī, whekī, wheki-ponga, whekī-kōhunga, wheki-kohoonga, whekī-ponga or golden tree fern	10	3.6
D. lanata subsp. *hispida*	Tūōkura, tūākura, woolly or stumpy tree fern	2	2
D. squarrosa	Atewheki, pakue, pēhiakura, tio, tirawa, tūākura, tūōkura, uruuruwhenua, wekī, whekī, rough, hard or harsh tree fern	8	3

limited; McGlone et al. (2010) showed that tree ferns have the largest ranges of all the New Zealand forest species. Spores are either dispersed by sporangial dehiscence or are retained in sporangia, which themselves detach from the fronds, and the spores undergo intrasporangial development adjacent to the parent plant providing for persistence in suitable habitat (Gastony, 1974; Conant, 1978).

Conant (1978) describes the volume of sporangia-captured spores of a single 8 m tall Caribbean tree fern *C. arborea* as being densest (per unit volume of air) up to 7.5 m from the sporophyte. Released free spores, in contrast, had a uniform density between 7.5 and 30 m (the most distant measurement) from the source plant (Conant, 1978). A study of hand-released Osmundaceae and Dryopteridaceae spores (54 and 45 µm respectively) in a forest habitat (Raynor et al., 1976), of, recorded dispersal distances of up to 100 m in regularly spaced spore traps. Peck et al. (1990) caution that estimates of dispersal ability in pteridophytes cannot be translated between taxa solely on the basis of size or mass of spores as such extrapolation overlooks potentially important dissimilarities in fecundity, habitat requirements, mating systems and gametophyte ecology. As New Zealand tree fern spores are similar in size (see above), and are released from similar heights (Table 1) it is suggested that they may be dispersed over comparable distances in a mature forest, and significantly greater distances in open vegetation.

The ability of tree ferns to successfully establish at long distance, however, has not been quantified. Korall and Pryer (2014) suggest that there is evidence for a causal relationship between breeding system and ploidy level (the requirement for outcrossing in diploids versus the ability to self in polyploids) with the success of long distance dispersal (distance not quantified) in Cyatheaceae. Successful dispersal over long distances is shown by a recent range expansion in *Gymnosphaera* (a group including tetraploid species) from South America into south-east Asia, compared to the dispersal of the proposed genus *Sphaeropteris* from Australasia into south-east Asia which, by their timings (43-36 mya), are most likely a product of vicariance (Korall and Pryer, 2014).

Spore viability ranges from two months (*Cyathea delgadii*) to 13 months (*Cyathea caracasana*, *Dicksonia sellowiana*), from species native to tropical regions of the Americas, compared to up to 22 years for the Australasian *Dicksonia antarctica* (Lloyd and Klekowski, 1970; Goller and Rybczyński, 2007) in a laboratory. No information is available on spore viability of the New Zealand tree ferns.

3.2. Conditions required for colonisation - establishment events

Little is known about either the establishment requirements of tree fern gametophytes or the conditions required for sporophyte development. Reis Moura et al. (2012) suggest that phosphorus is important for gametophyte development and sporophyte production. Small-scale (less than 25 cm^2) disturbance, such as removal of leaf litter and soil exposure/scarification, is important for the gametophytic establishment of terrestrial tropical fern species (Watkins et al., 2007), and is also necessary for the successful establishment of temperate species (Cousens, 1981). Therefore physical disturbance of soil surface may create a competition-free habitat, exposing extant spores in the soil, facilitating germination and tree fern dominance for decades if not centuries.

Cyclonic and tectonic disturbances are major drivers of regeneration in New Zealand forests, frequently inducing landslides and areas of wind-throw (Blaschke, 1988). Blaschke et al. (1992) described vegetation colonisation following landslides in Taranaki over a 25–40 year period during which the vegetation community was initially dominated by *D. squarrosa* and *C. smithii*. Wassilieff (1986) and Smale et al. (1997b) examined post-landslide successions in the drier East Cape region (half the annual rainfall of inland Taranaki; 1100 vs 2250 mm yr^{-1} respectively) dominated initially by *Kunzea robusta* alongside *C. dealbata* and *C. medullaris*; these latter two species are more drought tolerant (see supplementary information) than those recorded colonising the wetter Taranaki disturbance sites.

Studies into wind throw of forest trees describe *D. squarrosa* and *C. smithii* dominating canopy gaps for up to 30 years after initial ground fern cover, which lasts approximately two years (Adams and Norton, 1991). Studies of sites around fallen podocarps in Pureora Forest, west of Lake Taupo, have shown that these areas are rapidly colonised and dominated by *D. squarrosa* (Beveridge, 1973), which commonly establishes rhizomatously (Dingley, 1940). *C. medullaris* will gradually colonise *Paesia scaberula* and *Pteridium esculentum* fernland, weakening the fern canopy and permitting the establishment of seedlings of shrub and canopy species (Silvester, 1964; Wardle, 1991). Similarly, *D. squarrosa* establishes in level, fallow *P. scaberula* dominated pastureland, and forest succession initiates from 'islands' of the tree ferns (Silvester, 1964). This pattern contrasts with those that result in communities dominated by tree ferns (basal area in excess of 21.1 m^2 ha^{-1}), which are thought to have an inhibitory effect on succession (Walker et al., 2010; Richardson et al., 2014).

The disturbance created after logging of forestry plantations in New Zealand (generally *Pinus radiata*) may also result in the development of stands of *C. medullaris* (Fig. 2) with an associated shrub community of *Melicytus ramiflorus*, *Hedycarya arborea*, *Geniostoma ligustrifolium* and *Knightia excelsa* (Clarkson, 1986). Although *C. medullaris*, *M. ramiflorus*, and *G. ligustrifolium* have been recorded in *P. radiata* plantation understoreys (Ogden et al., 1997; Forbes et al., 2016), Australian studies indicate that tree ferns struggle to survive clear-felling events, and that regeneration of tree ferns is lower in these conditions than after natural disturbances (Ough and Murphy, 2004), indicating that *C. medullaris* would likely re-colonise after each rotation in plantation forests. Nevertheless, these observations still emphasise the role of tree ferns in pioneering communities.

Low intensity fires can lead to localised tree fern dominance because their apical growing stem are protected by a tight cluster of leaf primordia, allowing resprouting after burning (Ough, 2001) (Fig. 3). Pope (1924) and Wardle (1991) both record tree ferns reshooting after fire in New Zealand, with similar recovery recorded in Australian tree ferns (Ough, 2001). Ough (2001) also reports a greater abundance of *Cyathea australis* and *D. antarctica* in forests regenerating after wildlife than after clear-felling in southeast Australia. In contrast Watson and Cameron (2002) recorded *Cyathea capensis* in South Africa as experiencing high levels of mortality in response to fire, with juveniles (less than 150 cm height) as most susceptible. Tree ferns are fire-prone and are categorised as moderate-high flammability by the New Zealand Fire Service, indicating they will burn readily during moderate to high forest fire danger conditions and partially ignite during moderate conditions (Fogarty, 2001). This flammability is due to heavy accumulations of litter, elevated dead material and flammable green foliage on tree ferns (Fogarty, 2001). A physical assessment of frond material by Wyse et al. (2016) comparing plant trait flammability ranked *C. medullaris* as moderate, *C. dealbata* as moderate-high and *D. squarrosa* as having high flammability.

3.3. Gametophyte ecology

Little is known about the gametophyte ecology of tree ferns. The germination period for tree fern spores varies among species from a few days to several months whereupon they rapidly produce rhizoids, prothalli and become sexually mature within four months (Goller and Rybczyński, 1995; Kuriyama et al., 2004; Reis Moura et al., 2012); *in vitro* studies have shown that the length of time before a sporophyte is produced varies significantly (from 4 to 14 months) among species (Goller and Rybczyński, 2007).

Stokey (1930) found that under lower light levels (specific irradiance levels not described), the structure of the gametophytes of *C. dealbata*, *C. medullaris* and *C. smithii* are ameristic (i.e. become elongated and produce antheridia and archegonia at separate times, rarely progressing beyond the antheridial stage; the sex organs will be located terminally or laterally on the prothallia, rather than at the normal ventral location) reducing the chance of sporophyte production. Macro-nutrient availability also appears to affect the growth rate and pattern of tree fern gametophytes (Stephenson, 1907; Stokey, 1930; Kuriyama et al., 2004; Goller and Rybczyński, 2007; Reis Moura et al., 2012), however the response to specific nutrients remains unknown. Evidence of possible nutrient requirements of gametophytes is suggested by the distribution of the sporophytes on young, alluvial or volcanic soils (Aston, 1916; Wardle, 1991; Walker and Aplet, 1994; Coomes et al., 2005). However, extrapolating from the conditions supporting a mature sporophyte to those relevant for gametophyte ecology could be misleading as different biotic and abiotic filters may be involved.

3.4. Sporophyte ecology

Tree fern species are typically associated with fertile or semi-fertile soils over a range of hydrological conditions, slope, soil stability, forest-type or successional stages. However, a quantitative

Fig. 2. Dense *Cyathea medullaris* stand in the Hūnua Ranges south-east of Auckland established after plantation forest removal.

Fig. 3. A charred landscape one year post-fire with resprouting *C. dealbata* prominent in the landscape, Cornwallis Peninsula, west Auckland.

assessment of the environmental and biotic factors controlling tree fern distribution has not been undertaken. Correlative species distribution models suggest that the macro-scale distribution of tree ferns across New Zealand is largely determined by temperature (mean annual temperatures of 1.5–15.9 °C) and solar radiation (11.7–15.3 MJ m^{-2} day^{-1}) (Brownsey, 2001; Lehmann et al., 2002). The growth and reproduction of Australian tree ferns *C. australis* and *D. antarctica* have been consistently associated with temperature and precipitation (Forest Practices Authority, 2012; Syfert et al., 2013; Fedrigo et al., 2014).

Some New Zealand tree ferns are exceptionally cold-tolerant compared to most other tree fern taxa (Bystriakova et al., 2011b). For example, at Port Ross in the sub-Antarctic Auckland Islands (50°32′42″S 166°13′38″E) the southernmost populations of *C. smithii*, the tree fern with the highest latitudinal extent, experience a mean daily temperature of 2.9 °C during winter (de Lisle, 1965). New Zealand's tree ferns also show interspecific elevational habitat preferences (as a function of climate; Fig. 4a–d), with the species distribution along latitudinal and elevational gradients suggesting that temperature is a major niche discriminator. This pattern is most clearly seen in *Cyathea*, (Fig. 4a) with the upper elevational limits set by a minimum mean temperature of −4.9 °C.

While *Dicksonia* taxa do not appear to be differentiated by temperature preference, niche differences appear more strongly in relation to solar radiation, and it is likely that localised environmental factors, such as frost, also influence the location of *Dicksonia* both in the wider landscape and in relation to vegetation structures. Frost tolerance has been recorded for juvenile *D. fibrosa* (−8 °C), which is considered one of the more hardy New Zealand species, and can tolerate temperatures lower than *C. smithii* (−4.2 °C) (Warrington and Stanley, 1987; Wardle, 1991; Bannister, 2003). *D. fibrosa* will survive temperatures as low as −8 °C but not below −11 °C (Warrington and Stanley, 1987) and the species establishes and grows in edge habitat in elevated areas. The foliar frost resistance temperature for *D. squarrosa* is −6.5 °C (Bannister, 2003).

Lehmann et al. (2002) noted maximum tree fern diversity on steep slopes or on landslides; whether this is a product of soil conditions, light availability or simply site turnover is uncertain. Aston (1916) described *C. dealbata* as being prominent in developing scrub in steep volcanic ash ravines around Mount Tarawera. *C. colensoi*, *C. smithii* and *D. squarrosa* have also been associated with slopes supporting fertile soils (Wardle, 1991).

Community structure on chronosequences at Waitutu (291,000 years), Haast (6500 years) and Franz Josef (120,000 years), in South Island, New Zealand suggested a negative correlation between substrate age (and P availability) and the presence of tree ferns (Coomes et al., 2005; Richardson et al., 2005; Turner et al., 2012; Jangid et al., 2013). The youngest sand dune at the Haast chronosequence supported a community with *D. squarrosa* and *C. smithii* contributing 17–31% of the basal area. However, these species were almost entirely absent from older dunes (Turner et al., 2012, 2014), with tree ferns occurring only in those areas with relatively higher total phosphorus (181 year old dunes with 885 mg P kg^{-1} vs 4422 year old dunes with 492 mg P kg^{-1}). Coomes et al. (2005) recorded a strong positive relationship (r^2 = 0.78 and 0.58, respectively) between basal area (m^2 ha^{-1}) of *C. smithii* and *D. squarrosa* and total soil phosphorus. Furthermore, Coomes et al. (2013) suggest that *C. smithii* is a nutrient-demanding species, whereas *D. squarrosa* is a relatively low-nutrient tolerating tree fern species. This inference is supported by the forest community pattern along the Franz Josef chronosequence (Doblas-Miranda et al. (2008) where *D. squarrosa* was on older soils (60,000 years with soil C:P of 567.1) than *C. smithii* (250 years with soil C:P of 186.2), with both species absent from older successional communities (120,000 years with soil C:P of 743.3). Jangid et al. (2013) confirmed that tree fern basal area and total P were correlated along the Haast chronosequence. Combined, these studies support the conclusion that tree ferns are generally nutrient demanding, particularly in relation to phosphorus, with considerable inter-specific variation in nutrient niche breadth.

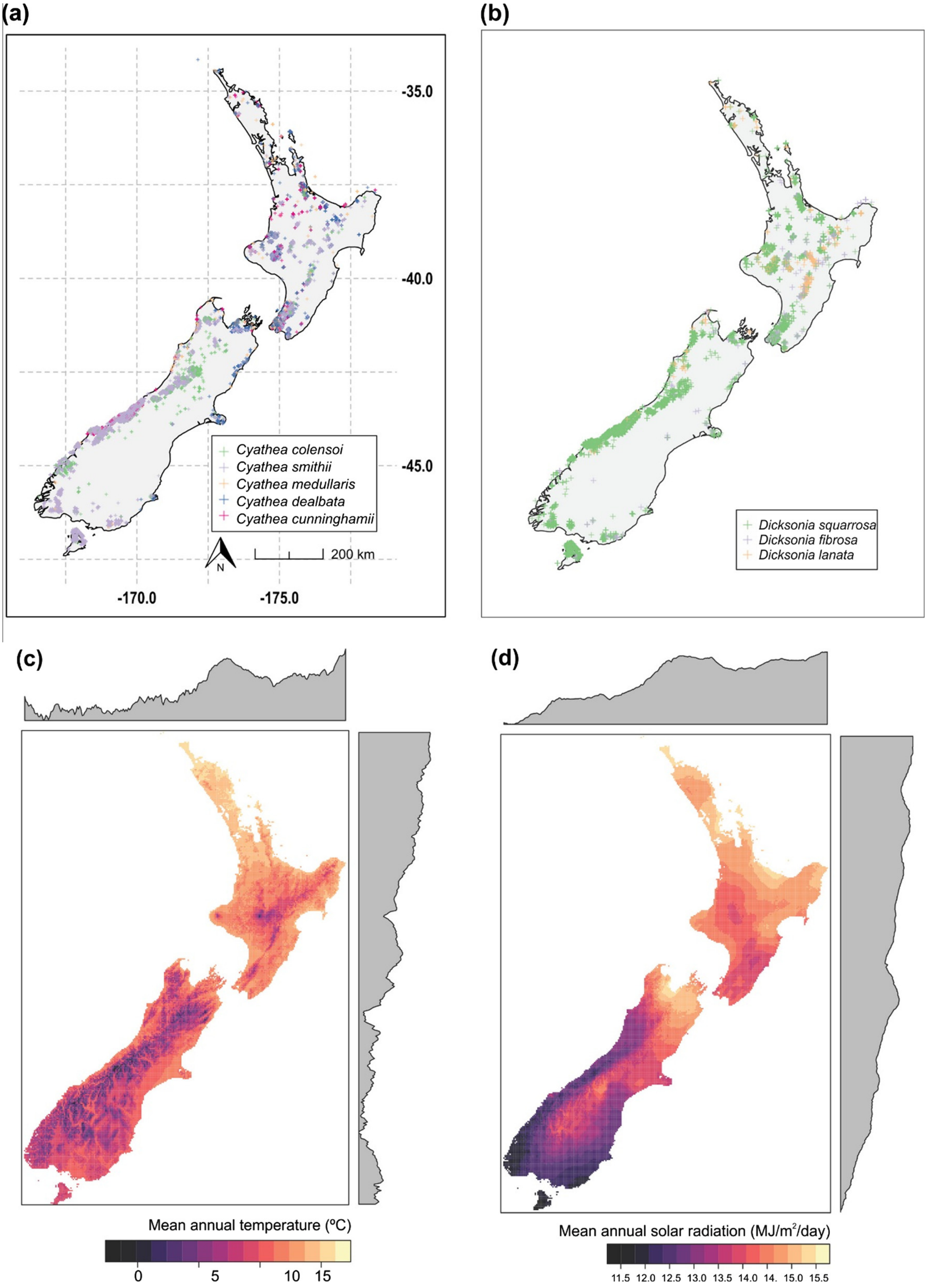

Fig. 4. (a–d) Presence-only distribution data (from (GBIF.org, 3rd August 2015)) of the New Zealand tree fern species: (a) *Cyathea* spp., (b) *Dicksonia* spp.; with mean annual temperature (c) and solar radiation maps (d) as key drivers of fern diversity in New Zealand (Lehmann et al., 2002). The grey histograms adjacent to (c) and (d) represent the mean of each column and row in the diagrams to emphasis overall trends. Figures a and b have been derived using presence-only data therefore any apparent distinctions between the distribution of the tree ferns species should be treated with caution as no corrections have been made for sampling bias (Syfert et al., 2013).

Both *D. squarrosa* and *C. medullaris* have been associated with boggy conditions (Dingley, 1940; Wardle, 1991). *D. squarrosa* is found in transitional communities between oligotrophic lowland mires and forest in Fiordland (Wardle, 1991). By comparison, *C. dealbata* is generally associated with free-draining soils (Pope, 1924; Wardle, 1991). Areas with poor drainage in *Dacrycarpus dacrydioides* – *Weinmannia racemosa* forest remnants in Westland (South Island, NZ) support *D. squarrosa* and *C. smithii* in greater abundance than drier patches of similar forest types (Miller et al., 2004). A similar trend was observed around the *Typha orientalis* swamps in the Waitotara and Wellington districts for *D. squarrosa* (Pope, 1924); however, specimens were showing signs of deterioration, e.g. short, wasted fronds, and appeared unable to survive with waterlogged roots. *C. medullaris* has been recorded both in bogs (Dingley, 1940) and dry forests (Pope, 1924) suggesting a tolerance for a range of moisture conditions. The Australian *D. antarctica* has a broad ecological niche and is capable of surviving in environments with a range of water supply conditions and evapotranspirational demands (Hunt et al., 2002). Hunt et al. (2002) identified extremely conservative water use, and the potential for the fronds of *D. squarrosa* to intercept rainfall and guide this water supply to adventitious roots at the stem apex as traits supporting this broad moisture tolerance.

Sporophyte distributions in NZ tree ferns also appear to be associated with irradiance gradients in forest and scrub communities (Table 2); this light response is also observed in Australia for *C. australis* and *D. antarctica* (Forest Practices Authority, 2012). Bystriakova et al. (2011a) reported that *C. dealbata* and *C. smithii* have near identical sporophytic demographics and leaf physiology, yet analysis of relative densities of the two species, in 30 × 30 m survey plots, indicates that they are spatially distinct in the landscape. Niche differentiation for these species may occur at the gametophytic stage (Bystriakova et al., 2011a). Experimental testing of growth and responses of gametophytes to controlled light conditions would address this hypothesis.

Extrapolation of ecological requirements based on current distribution in the landscape may also be confounded by actions of non-native pest species in New Zealand modifying tree fern distributions. Evidence of tree fern browsing by native New Zealand fauna is limited to coprolites of extinct upland moa (*Megalapteryx didinus*) that contain spores of *C. colensoi* (Wood et al., 2012). However, tree ferns are browsed by several introduced vertebrate herbivore species that affect their abundance locally (Mark et al., 1991; Nugent et al., 2002; Smale et al., 2008). *C. medullaris*, and to a lesser extent *C. smithii* and *D. squarrosa* are palatable and susceptible to brushtail possum (*Trichosurus vulpecula*) feeding (Ogden and Buddenhagen, 1994; Nugent et al., 2002). Direct browsing is less important that the indirect effect of competitive release of *C. dealbata* and *C. smithii* in the Orongorongo Valley (Fig. 1), the frequency of these species increased after brushtail possum browse removed dominance of more palatable species in the canopy (Campbell, 1990). Continued presence of brushtail possums in the area would transition the forest assemblage into a tree fern-shrub community (Campbell, 1990; Richardson et al., 2014). *C. colensoi* and *D. squarrosa* are susceptible to browsing by ungulates, and where these herbivores are abundant, tree ferns may die off (Veblen and Stewart, 1980; Mark et al., 1991; Wardle, 1991). However, *D. squarrosa* can resprout after disturbance (Martin and Ogden, 2006; Smale et al., 2008), which provides it with an advantage over the other tree fern species.

3.5. Influence in space – abundance of tree ferns in forest associations

Tree ferns are abundant in New Zealand's forest systems and can represent a significant proportion of the forest community in number of individuals (28–62%), basal area (2.3–41.7%) and biomass (3.8–21.0%) (Table 3). These data confirm that tree ferns are prominent in early successional communities in all of New Zealand's forest types and the understory of forest plantations (a list of vegetation communities with which tree ferns are associated can be found in supplementary materials). Similar levels of total biomass have been recorded from the tropical montane forest systems of Puerto Rico where *Cyathea bryophila* and *C. arborea*

Table 2
Forest type and structural position in which sporophytes of the New Zealand tree ferns have been recorded, along with maximum estimated age of sporophytes (ages reported by Bystriakova et al. (2011a) estimated by monitoring growth of tagged individuals over a 28 year period).

Species	Position in forest	Vegetation association	Max. age	Source
Cyathea colensoi	Sub-canopy/edge	Forest/alpine scrub	–	1, 7
C. cunninghamii	Sub-canopy	Gully forest	155	1, 2, 7
C. dealbata	Sub-canopy/edge	Forest/lowland scrub	250	1, 3, 4, 7
C. kermadecensis	Sub-canopy	*Metrosideros kermadecensis* forest	–	1, 7
C. medullaris	Canopy/edge	Disturbed ground/lowland scrub/tree-fall gaps/early succession remnant	100	1, 3, 5, 7
C. milnei	Sub-canopy	*Metrosideros kermadecensis* forest	–	1, 7
C. smithii	Sub-canopy/edge/canopy	Forest/scrub	250	1, 3, 4, 7
Dicksonia fibrosa	Canopy/edge	Scrub/forest	–	1, 3, 6, 7
D. lanata subsp. *hispida*	Sub-canopy	Kauri Forest	–	1, 7
D. squarrosa	Canopy/edge/sub-canopy	Disturbed ground/open scrub/forest	155	1, 3, 4, 6, 7

Sources: 1. Wardle (1991), 2. Brownsey (1979), 3. Pope (1924), 4. Wiser et al. (2011), 5. Large and Braggins (2004), 6. Dingley (1940), 7. Bystriakova et al. (2011a).

Table 3
Percent of total abundance, basal area and biomass of tree ferns in native New Zealand forests.

Source	Forest community	% Total abundance[a]	% Total basal area	% Total biomass[b]
Enright and Ogden (1987)	Secondary kauri *Agathis australis* forest	–	21.7	–
Burns and Smale (1990)	Secondary kauri *Agathis australis* forest	33.6 ± 1.9	20.5 ± 2.1	–
Kendall (Unpub. Data)	Secondary kauri *Agathis australis* forest	32.1 ± 7.9	20.0 ± 11.9	3.8 ± 5.0
Smale et al. (1997a,b)	Upland broadleaf/podocarp forest	34.2 ± 11.0	55.5 ± 34.0	–
McKelvey (1963)	Upland broadleaf/podocarp forest	36.9 ± 14.3	–	–
Daniel (1975)	Lowland broadleaf/podocarp forest	10.5	2.3	–
Ogden (Unpub. Data)	Lowland broadleaf/podocarp forest	46.3 ± 26.4	27.7 ± 4.0	–
Kendall (Unpub. Data)	Lowland broadleaf forest	28.3 ± 18.4	29 ± 16.6	8.1 ± 10.2
Kendall (Unpub. Data)	Early successional lowland forest	34.0 ± 20.7	41.7 ± 22.2	21.0 ± 11.9
Ogden et al. (1997)	*Pinus radiata* stands	62.8 ± 31.2	12.7 ± 12.1	–

[a] Stems ha^{-1}, mean ± 1 SD.

[b] Biomass estimated from volume of a cone calculated from DBH and height, canopy tree and tree fern height recorded in height classes and stem tissue densities obtained from Beets et al. (2012) and Richardson et al. (2014).

Table 4
Growth rates (cm yr^{-1}) of tree fern species from demographic studies, North Island of New Zealand.

Latitude/elevation	−41.33 S/130 m	−38.40 S/340 m	−37.09 S/100 m
[a]Mean ann. temperature (°C)	12.6	12.2	15.0
[a]Mean ann. precipitation (mm yr^{-1})	2505	1600	1600–2000
Cyathea cunninghamii	8.0 (7.0–9.0)	–	–
C. dealbata	3.2 (2.9–3.4)	5.0	11.0 ± 1.5
C. medullaris	11.5 (9.4–13.7)	18.0	–
C. smithii	3.4 (3.2–3.6)	–	11.2 ± 7.8
Dicksonia squarrosa	4.8 (4.3–5.4)	–	18.5 ± 2.9
Habitat type	Podocarp-broadleaved forest	*Pinus* plantation	Podocarp - broadleaved-forest
Reference	Bystriakova et al. (2011a,b)[b]	Ogden et al. (1997)[c]	Ogden/Burns (Unpublished data)[d]

[a] Data from CliFlo website [accessed 14.05.2016].
[b] 95% confidence intervals.
[c] No CI/SD values provided.
[d] ±1 SD.

represented 33% of the biomass of a site of post-disturbance regeneration (Weaver, 2008).

3.6. Influence in time – tree fern growth rates and survival

Tree fern growth rates vary between species and also with changes in light environments/successional stage, elevation and latitude (Table 4). The fastest growing tree fern species in New Zealand is *C. medullaris* (height increase of 18 cm yr^{-1} on the central highlands of the North Island); the growth rates of all species increase with decreasing latitude and increasing mean annual temperature.

Unpublished tree fern height data collected over a 34 year period from repeat-measure vegetation plots in the Kauaeranga Valley near Thames, provides long-term height growth rates for *C. dealbata*, *C. smithii* and *D. squarrosa* (Table 4). There is considerable intra- and inter-specific variability in growth rates at one site; changing light environments in response to shifts in canopy density is likely to explain some of this variation. Bystriakova et al. (2011a) identified a trade-off between growth-rate and shade tolerance in the New Zealand *Cyathea* with a faster-growing species *C. medullaris* restricted to higher light environments and having a low survivorship in shade (3.22% yr^{-1} mortality) compared to 0.69–1.85% yr^{-1} mortality for the slower-growing, more shade-tolerant *C. dealbata*, *smithii* and *cunninghamii*.

Ash (1987) found that *Cyathea* tree ferns surviving selective logging activities (in Fiji) may exhibit accelerated growth under the newly opened canopy. The ability of tree ferns to acclimate to significant changes in microclimatic condition following disturbance events has also been highlighted in the Australian tree fern *D. antarctica*, which is capable of producing fronds with ecophysiological characteristics that reflect the local conditions (Hunt et al., 2002).

Bystriakova et al. (2011a) attempted to age New Zealand tree ferns by monitoring tagged individuals over 28 years (Table 2) and estimated age ranges of up to 100 (*C. medullaris*) to 250 years (*C. dealbata*). Efforts to age individuals from various Australian tree fern species using radio-carbon (^{14}C) dating suggest that individual *D. antarctica* and *C. australis* may exceed 500 years in age (Mueck et al., 1996). It is possible that New Zealand tree ferns might be similarly long-lived.

4. The influence of tree ferns in forest communities

4.1. Evidence of effect

The ecosystem-level influences of tree ferns, such as their effects on species richness and diversity, composition and the surrounding structure of the forest, remain poorly understood in New Zealand. In Puerto Rico, tree ferns suppress forest regeneration on landslides by inhibiting the establishment and growth of woody species through competition for nutrients or light (Walker et al., 2010) and similar suppression effects in New Zealand are described below. As tree ferns mature, frond shedding (Gillman and Ogden, 2001; Gillman et al., 2002, 2004) alongside the deep layer of decaying fronds that accumulate in a mature stand will influence regeneration dynamics of woody species. Through their distinctive biochemistry, e.g. low Ca concentrations which slow decomposition and therefore mineralisation rates (Amatangelo and Vitousek, 2008), dead tree fern fronds are also likely to have a distinct influence on nutrient cycling processes (Richardson and Walker, 2010) (Fig. 4).

There is evidence for tree fern suppression of conifer and angiosperm woody species in New Zealand, as well as overseas (Drake and Pratt, 2001; Walker et al., 2010); Duncan (1991, 1993) cites Wardle (1974) who describes an absence of juvenile *D. dacrydioides* in a wind-throw gap in South Westland due to localised *D. squarrosa* and *C. smithii* dominance. The suppression of podocarp regeneration by *D. squarrosa* was also observed post-logging in podocarp-*Beilschmieda tawa* forests (Smale et al., 1987). McKelvey (1952) recorded restricted podocarp regeneration forests where tree ferns (and hardwood scrub) were prevalent and concluded that tree ferns were responsible. Norton (1991) evaluated podocarp seedling and sapling distribution patterns beneath podocarp, broadleaved and tree fern canopies, and showed that although tree ferns represented 25% of the basal area of the plot, less than 0.4% of all seedlings recorded in the plot were within the drip-line of tree ferns. Although suppression has most commonly been reported as influencing podocarp species, Burns and Smale (1990) observed that the establishment of woody species (e.g. *Weinmannia silvicola*, *Dysoxylum spectabile*, *K. excelsa*) was inhibited beneath a dense *C. dealbata* canopy on the lower valley slopes of a secondary *Agathis australis* – *Phyllocladus trichomanoides* forest stand on the Coromandel Peninsula.

4.2. Mechanism – macro-litterfall and shading

Tree ferns in New Zealand exhibit several modes of frond excision:

i. Retention: those that retain senescent fronds intact and entire at the base of the crown forming a dense persistent skirt; represented by *D. fibrosa*.
ii. Partial-retention: those that retain the stipe (rachis) of the senescent frond only, the pinnae decaying and falling from the fronds; represented by *C. smithii*.
iii. Shedders: those that excise and drop the entire senescent frond from the base of the stipe. All eight of the other arborescent tree fern species in New Zealand are shedders.

It is not known why frond excision behaviour varies between tree fern species. Page and Brownsey (1986) theorised that frond retention protects the growing crown from epiphytes and climbers. In comparison, Pope (1926) suggested a mechanism for epiphyte reduction that was the product of frond shedding in the relatively long (more than 30 cm) sections of stipe that are retained by *D. squarrosa*. The effects of the different excision behaviours do, however, influence the seedling communities beneath tree ferns.

Tree fern fronds of shedders comprise macro-litterfall (Gillman and Ogden, 2001) and create local disturbance beneath adults when they fall, restricting seedling establishment (Gillman et al., 2004). Litter damage to woody seedlings varies with seedling size, community composition and structure (Clark and Clark, 1989; Gillman et al., 2004); increasing tree fern macro-litterfall strongly correlates with an increase in vascular plant seedling mortality (Gillman et al., 2004). The regular frond shedders *C. dealbata*, *C. medullaris* and *D. squarrosa* (along with the palm *Rhopalostylis sapida*) have been recorded as being responsible for up to 14% of seedling mortality along 100 m forest transects (Gillman et al., 2004). The sheer depth of frond litter around tree fern stands, which can be up to 90 cm deep (Brock, Unpublished raw data), will suppress seedlings under tree fern canopies (Beveridge, 1973; Gillman et al., 2004); an absence of seedlings is particularly notable beneath *D. squarrosa* and *C. medullaris*, both of which can form dense stands or thickets (Fig. 2).

Forbes et al. (2016) experimentally removed tree ferns from forestry plantations to assess their influence, via shading, on the woody seedling community. This modification of the understory resulted in a significant increase in growth rates of the seedlings of the two canopy species present: *Podocarpus totara* and *Pittosporum eugenoides* (2.6-fold and 1.5-fold respectively). Burton and Mueller-Dombois (1984) undertook a tree fern frond removal experiment in Hawai'i and recorded an increase from 10.1% to 42.8% of incident radiation on the forest floor immediately below the de-fronded tree ferns. The increase in light levels and implied competitive release following the removal of the tree ferns provides support for the suggestion made by Coomes et al. (2005) that shade cast by tall ferns contributes to the restriction of regeneration opportunities.

4.3. Mechanism - influences on nutrient cycling

Richardson et al. (2005) and Vitousek et al. (1995) have shown that *D. squarrosa*, *C. smithii* and *Cibotium* spp. (the latter studied in Hawai'i) inhabit a wide soil fertility gradient (from 1 to 5 mg P kg^{-1} and 15 to 110 mg N kg^{-1}) and can deposit relatively high levels of nutrients in their litter; studies of Hawai'ian tree ferns show that they capture and retain relatively high proportions of nitrogen (twice that of canopy trees) and phosphorus (up to three times canopy trees) in early successional communities (Balakrishnan and Mueller-Dombois, 1983; Walker and Sharpe, 2010). Tree fern frond litter has a mean nitrogen content of 0.83% dry mass, compared to that of associated angiosperms (0.54%) and conifers (0.57%), but there appears to be relatively little difference in litter P across these plant groups (Enright and Ogden, 1987; Richardson et al., 2005). While increased foliar nitrogen will enhance litter decomposition, the availability of calcium can limit decomposition rates and interactions with invertebrates (McLaughlin and Wimmer, 1999; Silver and Miya, 2001; Hobbie et al., 2006); non-polypod ferns in Hawai'i (Amatangelo and Vitousek (2008) have higher N:Ca ratios than angiosperms. Enright and Ogden (1987) recorded a N:Ca ratio in *C. dealbata* 3.5-times greater than that in associated angiosperm species (14.8 vs 3.7 for *Vitex lucens*) indicating the potential for slowing litter decomposition and delaying the release of nutrients. Thus, communities supporting relatively high abundances of tree ferns might experience delayed release of nutrients from decomposing organic matter, but this dynamic requires further empirical investigation.

The decomposition rates of fern litter vary widely (Richardson and Walker, 2010). Amatangelo and Vitousek (2009) found that leptosporangiate fern fronds in nutrient-poor environments decomposed more slowly than angiosperms leaves. Shiels (2006), working in Puerto Rico, compared the decomposition rates of a pioneer tree (*Cecropia schreberiana*) with those of a pioneer tree fern species (*C. arborea*) and found the latter decomposed significantly more quickly (*Cyathea*: $k = 0.93 \pm 0.06$; *Cecropia*: $k = 0.68 \pm 0.06$, where k = decomposition factor). Enright and Ogden (1987), in their study of the decomposition dynamics of *A. australis* forest associates, compared the rate of decay (loss of mass over time) of the stipe of *C. medullaris* to the leaf blades of a number of common woody species, and found that the stipe decayed significantly more slowly, reflecting its sclerophyllous nature.

4.4. Mechanism - allelopathic effects

Cambie et al. (1961) tested for the presence of phytochemicals in New Zealand tree fern species (stem material and frond samples) focussing on compounds that affect herbivores, for example leucanthocyanins, which were recorded in *D. squarrosa* (frond and trunk), *D. fibrosa* (frond and trunk), *C. medullaris* (trunk, but not the frond) and *C. smithii* (frond and trunk). The trunks of *C. milneii* and *C. kermadecensis* were found to contain saponins, while samples of *D. lanata* (treated as a single species) and *C. colensoi* tested negative for alkaloids. Other phytochemicals that may have allelopathic effects, include secondary metabolites such as terpenoids and phenolics (Inderjit, 1996), but these were not considered by Cambie in his assays.

Froude (1980) showed that aqueous extracts from green frond material of tree ferns (*C. medullaris*, *C. smithii*, *D. squarrosa*) stunted the radicle development of salad cress (*Lepidium sativum*); and *C. medullaris* extract caused stunting in kakabeak (*Clianthus puniceus*) radicle growth. Froude observed similar inhibitory effects of the leachates of the three tree fern species on the seedling germination and growth of *W. racemosa*. Although not conclusive, Froude's studies suggested that tree ferns may influence species establishment through the presence of alkaloid phytochemicals in their fronds and trunks. In general little is known about allelopathy in New Zealand forests (but see Michel et al. (2011), Morales (2015)) and therefore any comment on the relative importance of any possible allelopathic effects of tree ferns on the forest community remains speculative at this point.

4.5. Mechanism - establishment surfaces for epiphytes

Tree fern trunks increase the available establishment surface area of a forest, with the root mantle of the trunk suitable for seed and spore adherence and germination (Beever, 1984; Leitch, 1997; Moran et al., 2003; Mehltreter et al., 2005). Tree ferns often provide advantages above the forest floor for seedlings where they may be protected from herbivory, low light levels, low soil fertility, macro-litterfall and deep leaf litter (Veblen and Stewart, 1980; Wright and Cameron, 1985; Smale and Kimberley, 1993; George and Bazzaz, 1999; Coomes et al., 2005; Wardle et al., 2006; Gaxiola et al., 2008). Species that establish on tree fern trunks are those species with small, wind-dispersed seeds that on the forest floor preferentially establish on exposed subsoil but are unable to establish in deep litter, e.g. *Weinmannia* spp. (Beveridge, 1973; Bellingham and Richardson, 2006).

Epiphytism on tree fern trunks by regenerating canopy tree species has been recorded worldwide including in the Mascarenes (Derroire et al., 2007), the Caribbean (Newton and Healey, 1989), Australia (Ashton, 2000; Bowkett, 2011), North America (Mehltreter et al., 2005) and New Zealand (Gaxiola et al., 2008). However, epiphytes on tree ferns are constrained by regional climactic limitations (Roberts et al., 2005); for example, epiphytic establishment appears to be more successful (24% of tree fern stems had seedlings ⩾ 15 cm high) and a more important pathway for canopy species regeneration on the wet, west coast of New Zealand, than it does on the relatively drier east coast (up to 1.5% of stems supported seedlings ⩾ 15 cm high) (Gaxiola et al., 2008; Richardson et al., 2014).

The most common successional pathway through epiphytic establishment on tree ferns in New Zealand involves the widespread angiosperm canopy trees *W. racemosa* and *W. silvicola* Cunoniaceae (Beveridge, 1973; Blaschke et al., 1992; Burrows, 2006). Hemi-epiphytism is apparent in up to 60% of *Weinmannia* canopy trees at some sites in Waitutu (Gaxiola et al., 2008). In dense forest communities, tree ferns, in particular *D. squarrosa* (Pope, 1926; Wardle and MacRae, 1966) and *C. smithii* (Lusk and Ogden, 1992; Smale and Kimberley, 1993), form an important establishment surface for regenerating *Weinmannia* spp. in conditions where *Weinmannia* would not be able to establish successfully on the forest floor. Oliver (1930) and Pope (1926) provide observational data from the Wellington region that *Pseudopanax arboreus*, *Raukaua edgerleyi*, *W. racemosa*, *Ackama rosifolia* and *C. grandifolia* survive to maturity as epiphytes on tree ferns. Regeneration of many canopy species (e.g. *Myrsine chathamica*) on the Chatham Islands depends on epiphytic establishment on tree ferns (Wardle, 1991).

5. Use and management of tree ferns

Historically tree ferns have been used in a variety of ways by indigenous communities throughout the southern temperate biome. Food storage pits would be lined with hard plates of *C. medullaris* by Māori in New Zealand (Anderson, 2000) to protect against rodent ingress; *D. sellowiana* was used by Guaraní communities in northern Argentina to treat disease and sclerenchyma tissue used to make arrowheads (Keller et al., 2011). Tree ferns were also used medicinally and as a regular component of diet: indigenous communities of south-eastern Australia would cook the pith of *C. australis* and *D. antarctica* (Nash, 2004); similarly in New Zealand the consumption of *C. medullaris* was a common source of carbohydrate (Leach, 2003).

The first record of trade in tree ferns is their apparent use as ballast in sailing ships carrying cargo from Australia to Great Britain (Page, 2004); because their stem density would not lend them to functioning effectively as ballast it is suggested they were used to line the hold to protect the cargo. Tree ferns (*D. squarrosa*, *D. fibrosa* and *C. medullaris*) were regularly harvested from the old growth *Pinus* plantations of the central North Island of New Zealand during the 1980s, supporting an industry worth some $2.75 M year^{-1} (Veale, 1986). Similar salvage operations were being undertaken from forests in south-eastern Australia where *D. antarctica* was collected and exported (Vulcz et al., 2002). Extraction of tree ferns from native and plantation forests in New Zealand and Australia has not been deemed sustainable either ecologically (Lawson, 2002) or economically, and tree fern nurseries have been established in Tasmania and Victoria in Australia (Unwin and Hunt, 1997; Ogle et al., 2000; Vulcz et al., 2002; Forest Practices Authority, 2012). While tree ferns are frequently harvested in Australia for the ornamental plant market (Vulcz et al., 2002), tree ferns are commonly used in New Zealand for fencing, stakes and garden pots (Veale, 1986). No information is available on modern use or extraction of tree ferns in Southern Africa or South America.

While active management of tree ferns has not been reported from productive forests, native or plantation, in the southern temperate region, the suppressive influence of tree ferns on seedlings, particularly of shade-intolerant species, could inhibit crop tree regrowth in forests where native hardwoods are selectively cropped (Carswell et al., 2007; Forbes et al., 2016). Where tree ferns dominate early successional communities this effect could diminish establishment potential of tall tree species and may leave systems vulnerable to exotic invasion (Walker et al., 2010; Richardson et al., 2014), suggesting potential benefits with regard to controlled local management of common tree fern species. The only published example of the active management of tree ferns in forest systems comes from tropical Hawai'i where non-native invasive tree ferns have had profound effects on soils and growth of native plants and have been the subject of selective management (uprooting, herbicide application) (Chau et al., 2013; Loh et al., 2014).

6. Conclusions

6.1. Do tree ferns influence forest composition and structure?

Tree ferns are an ancient, widespread and significant component of the indigenous forests of New Zealand and many other countries across southern temperate biomes, and play an important part in forest dynamics and ecosystem function. Characteristically they dominate early and mid-successional stages of the forest community after disturbance on more fertile soils, and may suppress regeneration of several associated canopy angiosperms and conifers.

Tree ferns may alter angiosperm community structure by influencing seedling composition within their drip-line, and therefore, where they are abundant, the successional trajectory of the forest community as a whole. It is evident that tree ferns provide a different successional pathway compared to other trajectories involving early successional woody forest species such as *K. robusta* – *Leptospermum scoparium* or *Metrosideros excelsa* scrub (Pope, 1924; Wardle, 1991; Sullivan et al., 2007). Understory tree ferns *C. dealbata* and *C. smithii* have a considerable influence on the forest community through their effects on nutrient cycling, formation of deep organic layers and by their physical impacts of their macrolitterfall on the regeneration niche. The regeneration of canopy tree species via epiphytism on tree fern trunks provides a successional pathway for some species, e.g. *Weinmannia* spp., but is mediated by local climatic conditions.

6.2. Future research priorities

Long-term data following the fate of tree fern individuals is lacking, with the majority of studies based on snapshot measurements of mature tree fern individuals. This approach is limited and does not provide information on key ecological events such as the point of entry of tree ferns into succession, and the length of time a cohort is present in a particular community. This narrow view is problematic given the longevity of individual tree ferns (potentially > 350 years), the difficulty in ageing individual tree ferns, and the uncertainty around the events and conditions that trigger their establishment. Dynamic forest models may provide a means of understanding the long-term effects of tree ferns in communities, and scaling issues (Perry and Millington, 2008). The uncertainties around establishment conditions are particularly pertinent when considering the likely influences of these species on successional processes in forest; data obtained from a narrow temporal sample represents a particular section of the life-history and role of a species and will not define a regeneration mechanism (Smale et al., 1997a). A comprehensive picture of the ecology of tree ferns requires an understanding of how life-history traits of the various species respond to particular sets of biophysical conditions over time (Nakashizuka, 2001), and this

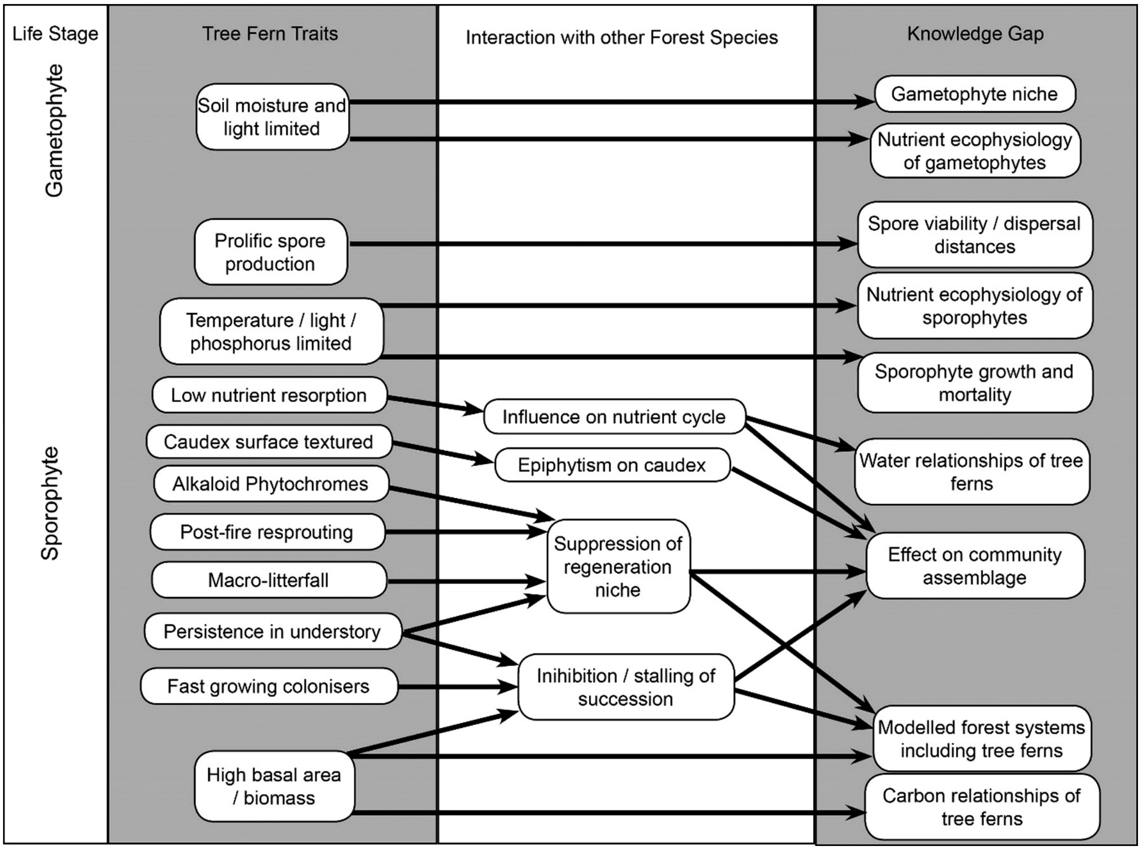

Fig. 5. A summary of the published information on the ecology and synecology of the New Zealand tree ferns highlighting research recommendations that will advance our understanding of tree fern influence on forest composition and structure.

requires long-term monitoring of individuals along environmental gradients.

Our synthesis of the ecology and function of New Zealand's tree ferns highlights important gaps in our knowledge of these important components of New Zealand's forests and of those across the southern temperate biome (Fig. 5). Future research of tree-fern ecology should consider both the autecology and synecology of these taxa, for example: (i) laboratory experiments manipulating environmental conditions for developing gametophytes; (ii) field surveys to obtain data on the selective effect on seedling recruitment by tree fern canopies; and, (iii) modelling forest systems to compare regeneration in the presence and absence of tree ferns in the community. Resolving these knowledge gaps will clarify our fundamental understanding of tree fern ecology, particularly with regard to their role in forest regeneration dynamics in southern broadleaf-podocarp forests, and with regard to their influence on forest systems under silviculture.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.05.030.

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