

NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

The invasion of non-native epiphyte *Platycerium bifurcatum* in Auckland's urban forest canopy

Jason Wu[1] and James Brock[1]*

[1]School of Biological Sciences, University of Auckland, Auckland, New Zealand
*Author for correspondence (Email: j.brock@auckland.ac.nz)

Published online: 27 September 2023

Abstract: New Zealand has been subject to extensive plant introductions since the 1840s leading to c. 2700 naturalised plant taxa including 500 serious environmental weeds. To date, non-native plant invasions in New Zealand have not included epiphytic invasions in forest canopies. Numerous records indicate non-mediated naturalisation of individuals of the non-native epiphytic fern *Platycerium bifurcatum* have been made; further, recent survey work on urban epiphytes identified a number of juveniles across the Auckland isthmus. To investigate the extent of *P. bifurcatum* naturalisation across Auckland we identified 30 mature plants of varying sizes that had been planted across the Auckland isthmus on both public and private land using iNaturalist NZ. A further 46 mature plants were identified during field surveys and whilst driving between field sites. All adult plants were measured and all publicly accessible walls and trees for up to 100 m around each plant were checked for juvenile plants. We recorded 104 juvenile (naturally established) plants; all but 19 had at least two publicly accessible adults within 100 m. *Platycerium bifurcatum* is establishing on trees with fissured or cracked bark-types and on scoria walls. Where large, fertile specimens of *P. bifurcatum* occur within 100 m, and suitable surfaces are available, this non-native epiphyte is successfully establishing in Auckland's urban forest canopy. The potential for this non-native epiphyte to spread into native forest ecosystems is not assessed in this study; however, key risks are highlighted along with suggested next steps to monitor and potentially control *P. bifurcatum* before this fern can invade.

Keywords: epiphytic habit, fern, invasive, naturalisation, non-native plant, pteridophyte, urban

Introduction

New Zealand has an order of magnitude more introduced (non-native) plant taxa (c. 25–35 000) than native plant taxa (c. 3700 excluding macroalgae; Duncan & Williams 2002; NZPCN 2023). Introductions of plant species started with the arrival of humans in the 13th century; however, initial introductions were few (c. six taxa; Horrocks 2004; Wilmshurst et al. 2008). Plant introductions significantly increased after the start of settler colonisation in 1840 and by 2002, 24 774 taxa of seed plants alone were known to have been imported into New Zealand (Duncan & Williams 2002). Not only do non-native plant taxa represent c. 10% of the current total plant richness in New Zealand, c. 2684 non-native plant species (c. 11%) are now naturalised with up to 500 of these non-native plants (c. 2%) classified as serious environmental weeds (NZPCN 2023). In rural landscapes non-native plants represent 3% of taxa on average in forest plots; higher proportions of non-native plant taxa are present in disturbed ecosystems (Bellingham et al. 2014). In urban areas, e.g. Auckland, up to 5 % of saplings are weeds in forest vegetation plots and up to 28% of non-woody understorey species were weeds (Griffiths et al. 2021); further, the presence of non-native weeds in native forest is strongly correlated to those planted in adjacent urban settlements and gardens (Sullivan et al. 2005).

Amongst the plant taxa imported en masse over the last 182 years, very few have been obligate epiphytes that are capable of establishing in the wild; as such, the epiphytic habit has not been as affected by plant invasions in comparison to terrestrial and freshwater ecosystems (Kirby 2014). Although a range of orchids, ferns, and bromeliads (many of which are obligate epiphytes) are currently available for sale in garden centres across New Zealand, there is little evidence that, aside from intentional planting by members of the public, these epiphytes are naturalising across the country. However, non-native facultative epiphytes, in particular weed species (e.g. *Nephrolepis cordifolia*) are establishing in the epiphytic habit across urban areas as well as the non-native hemi-epiphyte *Ficus macrophylla*, and a range of accidental non-native epiphytes (e.g. *Ligustrum* spp.; Kirby 2014; Auckland Council 2020; Wu 2023). So, whilst some non-native and invasive plant taxa will establish as facultative or accidental epiphytes, there are currently no reports of non-native obligate epiphytes naturalising across New Zealand.

Platycerium bifurcatum is a non-native, obligate epiphyte that has been introduced into New Zealand and is native to Australia, Papua New Guinea, and the island of Java (Pemberton 2003). More commonly known as elkhorn or staghorn fern

DOI: https://doi.org/10.20417/nzjecol.47.3542

(also: elk / stag horn, elk's / stag's horn), *P. bifurcatum* is one of c. 15 species in *Platycerium* and is distinctive in forming genets (clonal colonies; hereafter colony) through asexual reproduction (most *Platycerium* spp. are solitary; Hoshizaki 1972; Kreier & Schneider 2006; Burns 2021). Dense colonies are effective in overcoming the various stressors of the epiphytic habit and individual ramets of *P. bifurcatum* can express different frond morphologies (on the basis of vertical position in the colony) thereby performing different functions for the colony (Burns 2021). Colonies can establish on vertical surfaces in the understory and mid-canopy and are not constrained by phorophyte taxa as an establishment surface (Solikin 2014; Dawes et al. 2020). As an attractive, ornamental taxa, this fern has been introduced to gardens around the world and is an invasive weed in Florida, South Africa, and Hawai'I (Wilson 1996; Pemberton 2003; Jones et al. 2020).

The earliest record of *Platycerium* in New Zealand is in a newspaper article describing a horticultural exhibition in Lyttelton in February 1867; the plant named is *Platycerium alcicorne*—a synonym of *P. bifurcatum* (The Press 1867). *Platycerium alcicorne*, *P. grande*, elkshorn, and stagshorn (likely referring to *P. bifurcatum* and/or *P. superbum*) originating "from New South Wales" and the forests of "the north-east coast of Australia" were regular horticultural show exhibits during the late 19th and early 20th centuries (The Press 1870; Lyttleton Times 1871; Otago Daily Times 1903; Wilson 1927). "Staghorn ferns" are recorded in gardens in Mount Eden, Auckland by 1904, "staghorn and elkhorn ferns" were advertised for sale by J. Bateson & Son of Hamilton in the Waikato Times by 1923, and in 1929 The Sun states that *P. alcicorne* is "easily grown in the cool greenhouse" in Auckland (New Zealand Graphic and Ladies' Journal 1904; Waikato Times 1923; The Sun 1929). The earliest listings for *P. bifurcatum* in the collections of New Zealand botanic gardens are 1958 (Christchurch Botanic Gardens) and 1961 (Wellington Botanic Garden; M. Dawson, Manaaki Whenua, pers. comm.).

The earliest record of possible natural establishment of *P. bifurcatum* was on *Ficus macrophylla* (at a height on a tree that suggested that this colony had not been planted) in Russell in 1988; and in 2003 in North Auckland, *P. bifurcatum* was recorded as having established on a cabbage tree *Cordyline australis* nearby a large mature colony (Heenan et al. 2004). Other phorophytes that this non-native fern has established on include loquat *Eriobotrya japonica* and pōhutukawa *Metrosideros excelsa* (Brownsey et al. 2021). There is some uncertainty as to the current status of naturalisation of this plant, requiring further work to establish whether specimens are deliberately planted or are establishing naturally (NZflora 2023).

Colonies of *P. bifurcatum* have been shown to be predominantly clonal in their natural range; however, individual plants from genetically distinct colonies can establish and grow in amongst host colonies (Burns et al. 2021). As most colonies in New Zealand will have established as an individual planting event, we consider it likely that ornamental plantings of this taxa will most likely be clonal and, unless multiple other mature plants are nearby in the landscape, fertile adult plants of *P. birfurcatum* in New Zealand are potentially sexually isolated. Whether *P. bifurcatum* gametophytes are capable of selfing to produce a new sporophytic generation is unknown, but the potential for this process to effectively establish new populations of many fern taxa is potentially overstated (Haufler et al. 2016).

Mature colonies of *P. bifurcatum* are now found scattered across Auckland as ornamental plantings and iNaturalist NZ records suggest that this species is establishing naturally nearby mature ornamental colonies on both street trees and scoria walls. Given the extensive planting of this taxa across the Auckland region (c. 40 records on iNaturalist NZ), and the relative maturity of these colonies (many are > 1 m across and support multiple plants), it is likely that if naturalisation is ongoing then this should be evident in Auckland on street and garden trees across the urban forest. After several juvenile plants of *P. bifurcatum* were observed during field work in 2022 for a graduate research project on urban epiphytes, we decided to examine the current field evidence for the naturalisation of *P. bifurcatum* and consider the invasion risk to the epiphyte habit in New Zealand.

This study examines patterns of adult (planted) occurrence, juvenile (naturally established) plant occurrence, and considers the predictors of the establishment of *P. bifurcatum* across Auckland.

Methods

We collated iNaturalist NZ records for New Zealand (summarised in Table 1) and used these records to locate individual plants and colonies of *P. bifurcatum* across the Auckland isthmus (verifiable and casual; $n = 42$ total, but three records confirmed to be duplicates; iNaturalist NZ records used $n = 39$; Fig. 1). We then visited all extant plants where public access was possible ($n = 30$; 9 were not present or inaccessible) and examined all publicly accessible trees and walls within 100 m of the plant. We chose 100 m as the survey cut-off as (1) this represents twice the distance of juvenile occurrence from adult plants in Florida (the only published density data for *Platycerium*; Pemberton 2003). Where adult plants not recorded on iNaturalist NZ were observed either (1) within 100 m of a surveyed plant, (2) on Google StreetView, or (3) whilst driving around the city we included these in our study ($n = 46$).

The status of 'adult plant' was assigned where plants either (1) retained clear evidence of planting (method of attachment visible) or (2) were colonies that we conservatively

Table 1. A summary of iNaturalist NZ records of *Platycerium bifurcatum* across New Zealand.

iNaturalist NZ record type	*n*	Relative position	Location	Latitude	Longitude	Status
Verifiable	38	Northernmost	Russell, Northland	−35.261363	174.121437	Naturalised
		Southernmost	Wellington	−41.280664	174.768867	Naturalised
Casual	66	Northernmost	Kerikeri, Northland	−35.217307	173.962398	Planted
		Southernmost	Lincoln, Canterbury	−43.643421	172.467785	Planted

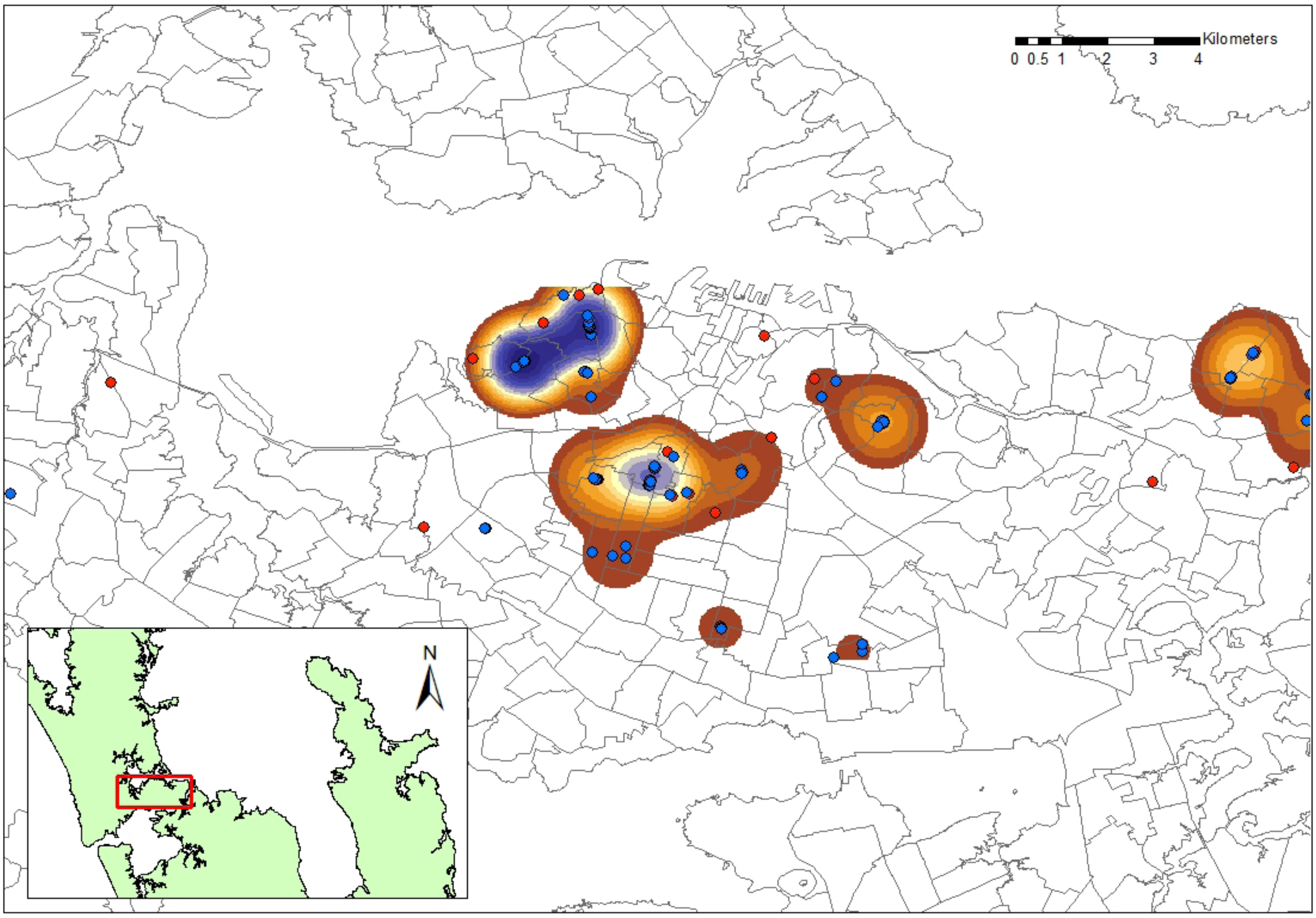

Figure 1. Planted *Platycerium bifurcatum* colonies across the Auckland isthmus (red = iNaturalist NZ record; blue = new colonies observed during survey work). Density kernel indicates density of all plants (adult and juvenile) recorded during survey work; note hotspots of *P. bifurcatum* in Mount Eden (lower centre), Westmere and Ponsonby (upper center), and St Heliers (far right). The kernel density map was produced using the spatial records of plants identified from iNaturalist NZ and during the survey work associated with this study, as such the blank areas of the map do not denote an absence of *P. bifurcatum*, merely the absence of observations.

assumed had developed from a historic planting event. We recorded the size of adult plants (height, width, depth; estimated visually to nearest 25 cm where not publicly accessible) and location (street address) and recorded the same parameters for any naturally established plants (juvenile) along with a global positioning system recording for the location of each plant. We also recorded the type of surface, taxa of host, and bark type or features (e.g. cracks, cement) of the host that any juvenile had established in/on.

Spatial analysis was undertaken in ArcMap™ 10.8.1. using the buffer and spatial join functions. Buffers of 10, 20, 50, and 100 m were established around juvenile plants and a single buffer of 100 m around adult plants; the numbers of adult and juvenile plants per adult buffer, and adult plants per juvenile buffer radius were then calculated. Where adults occurred within 100 m of one another they were classified as belonging to a group; adults occurring away from (> 100 m) of other adults were classified as lone. The location of the plants was updated to identify distinct groupings where these occurred on the same road, or in the same suburb.

A student's *t*-test was undertaken to examine the differences in colony size of two groups: adult plants in groups but with no juveniles vs adult groups that were associated with nearby juvenile plants. Linear models were used to examine whether (1) the occurrence of juvenile plants and (2) juvenile plant abundance was best predicted by adult colony size and/or adult colony frequency within 100 m. All analysis was completed in R using R studio (Allaire 2012; R Core Team 2015).

Results

We recorded 76 adults and 104 juveniles across the Auckland isthmus (a total of 180 plants; Fig. 1). Adults were planted either in the gardens of private properties (26), on street trees (37), or scoria walls (3), or planted into bush areas in reserves (11); phorophyte taxa were highly varied but driven by the dominant street tree plantings of the area. The greatest density of adult plants was in Wharua Reserve in Remuera where nine individual colonies were discovered; these plants were likely planted as they had been individually attached to native trees within regenerating native coastal forest. The most common tree taxa for *P. bifurcatum* plantings was the Indian bead tree *Melia azedarach* ($n = 29$) representing 38% of planting sites. Of the 76 adult plants 26 plants were classified as lone, and 50 plants were identified as occurring in one of 15 groups (mean plants per group ± SD: 3.3 ± 2.1) where more than one adult plant occurred within 100 m of at least one other adult plant.

Juveniles did not occur at all sites where an adult, or groups of adults were visible from publicly accessible areas; 29 adults across ten groups (of 15) were recorded having juvenile plants (n = 83) occurring within 100 m (Figs 1, 2; Table 2). The five (of 15) groups of adults that did not have juveniles within 100 m were likely constrained by either a lack of suitable establishment surface (e.g. a lack of street trees along Smythe Road, or the dominant street tree was flaky-barked London plane *Platanus* × *hispanica* along Herne Bay Road), or potentially inadequate propagule pressure (Wharua Reserve, Wharua Road, Hartland Avenue, and Eden Garden) where the (fertile) plants were significantly smaller (0.8 ± 1.9 vs 2.5 ± 3.4 m^3; $t_{(37.46)} = -2.22$, $p = 0.031$) than other adults that had juveniles within 100 m. Thirteen juveniles had two adults within 100 m, 26 had three adults, and 38 juveniles had four adults within 100 m (Fig. 3). Juveniles most commonly (96/104) occurred within 100 m of a group of adults (Table 2). In four locations, juveniles were recorded within 100 m of a lone adult (in Mount Albert, Mount Eden, Grey Lynn, and Ponsonby; Table 2). In five locations, juveniles were recorded with no adults within 100 m of their location (in Mount Eden, Westmere, Herne Bay, and Ponsonby). The linear models suggest that there is a significant relationship between increasing size (mean size per group) of adults and increasing adult density with juvenile occurrence ($F_{(3,35)}$ = 1.59, p = 0.081), but not with juvenile abundance ($F_{(3,35)}$ = 0.91, p = 0.446).

The mean number (± SD) of juveniles per phorophyte/structure was 2.7 ± 3.0, with a maximum number of 13 juvenile plants on a single *M. azedarach* in Ponsonby. Substrates on which juvenile plants were most commonly recorded was the street tree *M. azedarach* (n = 34; 89%), the second most common establishment surface being scoria walls (n = 3), and the third and final substrate that juveniles were recorded on was *Agonis flexuosa* (n = 1). Both the walls surface and phorophytes' bark are characterised by cracks, clefts, and cavities. The size distribution of the juveniles is strongly skewed suggesting either limited survival of juveniles or a recent increase in successful sporophyte production (Fig. 4); a total of four naturally established plants were recorded as having fertile fronds in Mount Eden (n = 2), Ponsonby (n = 1) and St. Heliers (n = 1).

Discussion

Our study highlights the frequent occurrence of planted fertile specimens of *P. bifurcatum* across the Auckland isthmus and that naturalisation is occurring with juveniles establishing at 22 separate locations across the central city. *Platycerium bifurcatum* is an admired garden plant (according to several members of the public and owners of specimens whom we spoke to during surveys) and mature plants have been regularly, now increasingly frequently, planted across the Auckland isthmus. Ongoing planting efforts by members of the public continue to introduce fertile plants onto garden and street trees as well as into native bush reserves. As a result of these efforts, this non-native epiphyte is naturalising and is starting to invade the urban canopy in Auckland. We started by surveying plants that were identified previously on iNaturalist NZ and that were publicly accessible; given that by driving around the central city we identified a further 46 adult plants we have likely sampled a very small proportion of those adult plants that occur across Auckland and will likely have missed many juveniles.

Platycerium bifurcatum appears to be constrained to naturalising only where there are at least two plants within 100 m; in this situation (if these plants are both fertile and established at their planting site) there is a high likelihood of finding a juvenile plant (with shield fronds up to 0.3 m^2) on rough surfaces clear of other vegetation. Nearby establishment of juveniles to parent colonies has also been observed in Florida where *P. bifurcatum* is an invasive species (Pemberton 2003). As colonies tend to be genetically identical, it is possible that juveniles are only produced where local spore rain provides opportunities for gametophytes of genetically distinct adults to sexually reproduce and produce a new sporophyte (Haufler et al. 2016; Burns et al. 2021). Although 19 juvenile plants were found with only one mature adult, and eight plants were found with no adults within 100 m, we consider it possible that (1) mature colonies are present within 100 m of these juveniles but they are not visible from the street or otherwise publicly accessible, or (2) that planted colonies originally comprised two different plants. We suggest that given the presence of well-established, large, but isolated plants (e.g. in Herne Bay) that have no juvenile plants nearby infers that large, clonal colonies are by themselves unable to support a new generation of sporophytes.

The surfaces that juvenile *P. bifurcatum* were recorded on were clear of other vascular vegetation (epiphyte/epimural) but all featured cracks, clefts, and cavities. Where juvenile sporophytes were recorded on scoria walls the sporophyte appeared to be attached to the mortar or, where mortar was absent, positioned between two stones. Juveniles on street trees predominantly occurred on the side of branches of trees with fissured bark. We suggest that cracks and fissures represent features that potentially could support an elevated spore bank and that where spore from multiple colonies aggregates there is increased potential for successful sexual reproduction. Further, gametophyte development may be supported by micro-niche conditions in the cracks in the substrate (Peck et al. 1990; Flinn 2007). Given the pH of walls and mortar is alkaline and that tree bark is commonly acidic (Spier et al. 2010; Elgohary et al.

Table 2. Isolation status of adult plants (i.e. whether an adult plant is located within 100 m of another or more adult plants) and whether juvenile plants of *Platycerium bifurcatum* recorded within 100 m (mean ± SD).

Status of adult	Number of groups	Number of adults	Volume of adults (m^3)
Lone with no juveniles	-	22	3.6 ± 4.6
Lone with juveniles	-	4	3.2 ± 3.4
Groups with no juveniles	5	21 (3.0 ± 3.0 group^{-1}*)	1.3 ± 2.2
Groups with juveniles	10	29 (3.6 ± 2.3 group^{-1})	2.5 ± 3.4

Figure 2. Top row: planted adult *Platycerium bifurcatum* on *Melia azedarach* (street trees) in Mount Eden; bottom row: naturally established juvenile plants on *Melia azedarach* (street tree) in Sandringham (left) and on a scoria wall in Mount Eden (right); images JW.

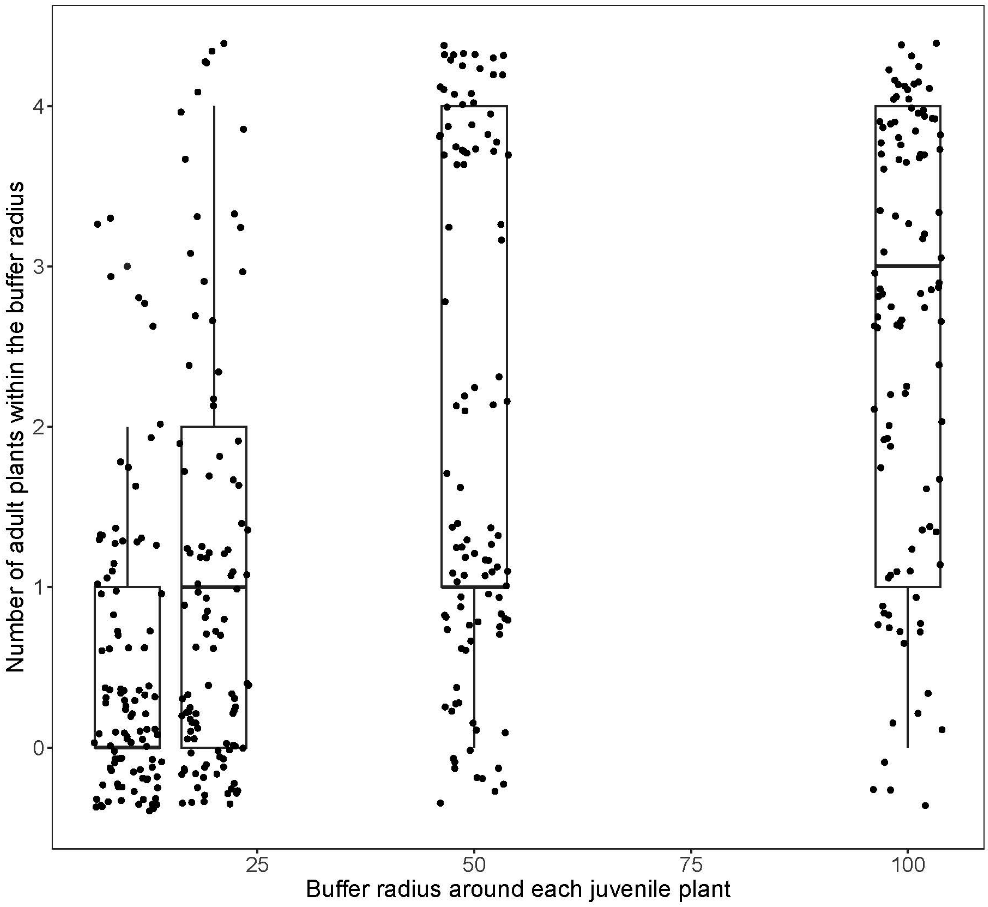

Figure 3. The number of adult plants occurring within 10, 20, 50, and 100 m of each juvenile plant recorded (jittered points represent number of adult plants; box and whisker plots show median and first and third quartiles).

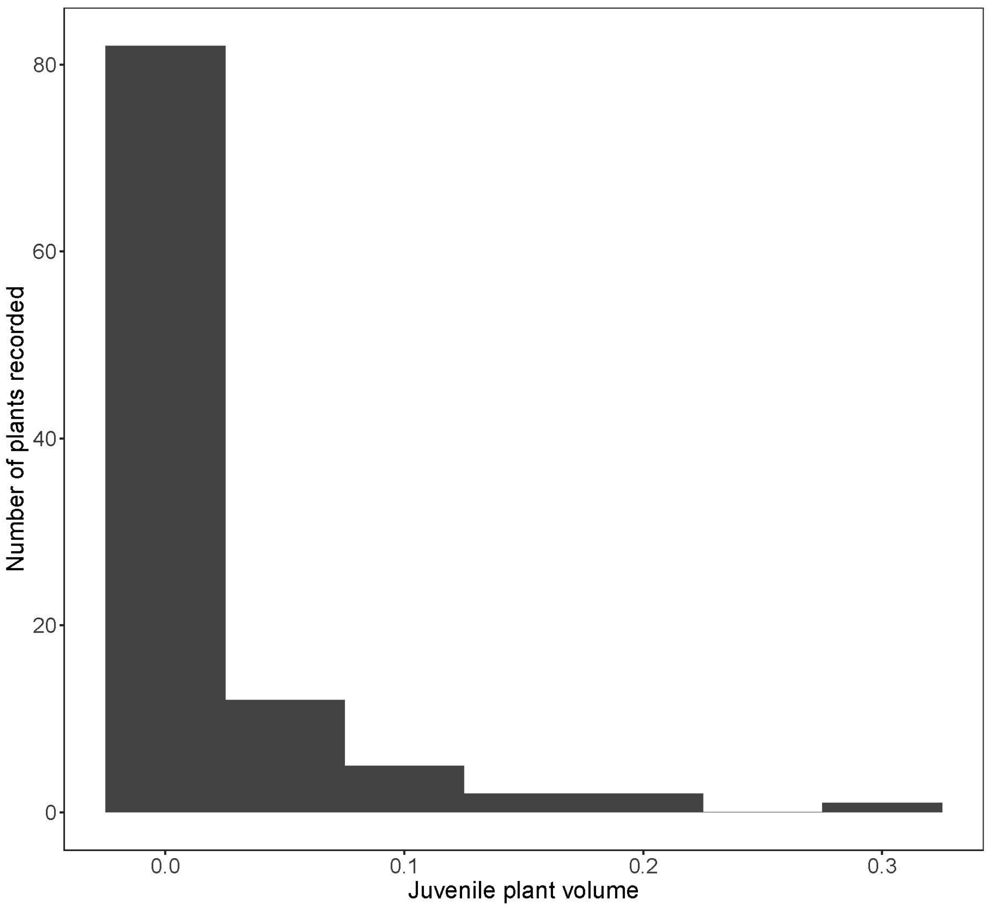

Figure 4. Size class distribution of juvenile *Platycerium bifurcatum* recorded across the Auckland isthmus; adult sizes for comparison: minimum = 0.08 m^3; range (5–50–95%) = 0.29–0.76–8.5 m^3.

2022; Kovářová et al. 2022), then we suggest that either pH is no constraint on establishment (comparing alkaline concrete to acidic pH of bark) or spore bank and water availability are potentially more significant constraints.

Urban ecosystems are complex, have an array of surfaces that are not available in natural ecosystems, and may not be indicative of establishment potential in native forests. However, *P. bifurcatum* appears not to be constrained by establishment surface: this fern will establish on a range of surfaces from exposed scoria walls through to the shade of the sub-canopy, from broad urban street tree branches to narrow, vertical stems and has been recorded on *Cordyline australis*, *Eriobotrya japonica*, and *Metrosideros excelsa* elsewhere in New Zealand (Heenan et al. 2004; Dawes et al. 2020; Brownsey et al. 2021; Wu 2023). In Indonesia, *P. bifurcatum* has been recorded growing naturally on 14 different species (of 12 families) at Purwodadi Botanic Garden (Solikin 2014). Once established, *Platycerium bifurcatum* forms large colonies and effectively can ameliorate the excesses of local environmental conditions meaning that this taxa is less constrained by stressors than other epiphytes (Jones et al. 2019). This plant is already a serious weed in Florida and Hawai'i and is considered a serious invasion risk across the Pacific (Space & Flynn 2002). In South Africa *P. bifurcatum* is becoming increasingly prominent in forested ecosystems and is displaying invasive behaviour; as such, this species is now listed as a species to be managed with high urgency (Jones et al. 2020).

Assuming that all adult individuals and colonies encountered during surveys were planted, *Platycerium bifurcatum* appears to be at the reproduction stage of establishment in Auckland, i.e. individuals are surviving and reproducing but have not yet established self-sustaining populations (although four juveniles are producing fertile fronds; Blackburn et al. 2011). This provides an opportunity to manage this potential sleeper weed before it fully establishes in Auckland and northern New Zealand (Blackburn et al. 2011; Hulme 2020). If this epiphyte were to establish and expand beyond the canopy of New Zealand urban forests there could be serious implications, particularly in the context of a changing climate (Sullivan et al. 2005; Sheppard et al. 2016). New Zealand native forests are already being invaded by non-native plant taxa such as ground cover plants, e.g. *Tradescantia fluminensis*, affecting regeneration; having an invasive species in the canopy would compound the negative effects of prior invasions as well as introducing new problems (Wilson 1996; Pemberton 2003; McAlpine et al. 2015). Large numbers of colonies in the canopy and subcanopy of native forests could potentially displace our native epiphytes (e.g. *Astelia* spp., ferns, orchids) creating novel habitats in the canopy for native and non-native epiphytes, invertebrates, and invasive mammals (Wilson 1996; Pemberton 2003; Innes et al. 2018; Allen et al. 2021). Further, studies from Lord Howe island in the native range of *P. bifurcatum* show that this taxa can establish on stems as small as 8 cm in diameter in the understory suggesting that New Zealand's rich small tree flora and palm understorey could provide ready suitable establishment surfaces in native forests (McGlone et al. 2010; Dawes et al. 2020).

Further work necessary to establish the risk to New Zealand's native forests from *P. bifurcatum* includes:
(1) Modelling work to understand the niche envelope of this taxa and the likely range of suitable environmental spaces in New Zealand including under future climate scenarios.
(2) More extensive field survey work of mature plants across the North Island to robustly establish the current extent of successful naturalisation.
(3) Field analysis of and experiments on bark types associated with successful epiphytic establishment and a comparison to bark types across the native range and common hosts of *P. bifurcatum*.
(4) Monitoring of trees and walls around Wharua Reserve in Remuera, Auckland, to identify when the dense plantation of adults in the regenerating native bush begins to produce successful new sporophytes, along with potential management/removal of adult plants.
(5) Long-term monitoring of juvenile plants across Mount Eden, Westmere, Ponsonby, and St Heliers (the largest clusters of successfully naturalising individuals) to identify growth and mortality rates of juveniles.

Our study is not based on stratified sampling: a combination of iNaturalist NZ, Google StreetView, and chance identification whilst driving does not permit us to establish the density of mature *P. bifurcatum* across the city. However, haphazard sampling has highlighted the high density of individuals of this plant in Mount Eden, Sandringham, Westmere, Ponsonby, and Glendowie and as such, although the numbers of adult and juvenile plants recorded across the city were not large, we suggest that if the juveniles recorded persist to form fertile fronds, then this non-native epiphytic fern will soon establish the first self-supporting populations in New Zealand. Whilst data on time to maturity (spore-production) for this species is scarce, Hughes (1984) suggests that the "Majus" variety can grow from spore to maturity in between five and seven years and horticultural websites suggest that *P. bifurcatum* can take up to ten years to mature (e.g. Planterina Holdings LLC 2023). The mortality rate of juveniles across the city is currently unknown and a more robust understanding around risk to urban and indigenous ecosystems from *P. bifurcatum* needs to be developed. At the time of writing, we believe that it is possible to manage and control *P. bifurcatum* across Auckland and New Zealand to prevent this fern from invading; however, controlling the horticultural trade and private planting of this popular species may prove challenging (McGlone et al. 2014; Groenteman 2022). If this species successfully captures space in the urban forest canopy of New Zealand cities, then it is likely only a matter of time before this species will establish in our indigenous forest ecosystems (Pemberton 2003; Sullivan et al. 2005; Jones et al. 2019).

Acknowledgements

The authors would like to acknowledge the University of Auckland for supporting the field work through the postgraduate student allowance (JW), and the School of Biological Sciences new staff development fund (JB). We would especially like to acknowledge Murray Dawson (Manaaki Whenua) for support in identifying records relating to the arrival of *Platycerium bifurcatum* into New Zealand and also the two anonymous reviewers who provided many constructive and very useful comments.

Additional information and declarations

Author contributions: JW and JB developed the method and undertook the field survey work and analysis. JB led the writing and JW reviewed, edited, and completed the manuscript.

Funding: This research was funded by the University of Auckland, School of Biological Sciences new staff development funds.

Data and code availability: The location data of all plants recorded in this study is in the Supplementary Material.

Ethics: No ethics required to undertake this work.

Conflicts of interest: The authors declare no conflicts of interest.

References

Allaire J 2012. Rstudio: integrated development environment for R. Boston, MA. http://www.rstudio.com/

Allen WJ, Waller LP, Barratt BIP, Dickie IA, Tylianakis JM 2021. Exotic plants accumulate and share herbivores yet dominate communities via rapid growth. Nature Communications 12(1): 2696.

Auckland Council 2020. Mahere ā-rohe whakahaere kaupapa koiora orotā mō Tāmaki Makaurau | Auckland regional pest management plan 2020-2030. Auckland, Auckland Council. 486 p.

Bellingham PJ, Richardson SJ, Gormley AM, Husheer SW, Monks A 2014. Department of Conservation biodiversity indicators: 2014 assessment. No. LC1957. Lincoln, Landcare Research. 116 p.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26(7): 333–339.

Brownsey PJ, Parris BS, Perrie LR 2021. Flora of New Zealand: ferns and lycophytes. 2nd edn. Fascicle 1, Polypodiaceae. Flora of New Zealand [electronic resource]. Lincoln, Manaaki Whenua Press. 76 p.

Burns KC 2021. On the selective advantage of coloniality in staghorn ferns (*Platycerium bifurcatum*, Polypodiaceae). Plant Signaling & Behavior 16(11): 1961063.

Burns KC, Hutton I, Shepherd L 2021. Primitive eusociality in a land plant? Ecology 102(9): e03373.

Dawes TN, Hutton I, Burns KC 2020. Spatial ecology and host diversity of three arboreal plants from Lord Howe Island. Australian Journal of Botany 68(6): 458–465.

Duncan RP, Williams PA 2002. Darwin's naturalization hypothesis challenged. Nature 417: 608–609.

Elgohary YM, Mansour MMA, Salem MZM 2022. Assessment of the potential effects of plants with their secreted biochemicals on the biodeterioration of archaeological stones. Biomass Conversion and Biorefinery: https://doi.org/10.1007/s13399-022-03300-8.

Flinn KM 2007. Microsite-limited recruitment controls fern colonization of post-agricultural forests. Ecology 88(12): 3103–3114.

Griffiths GJK, Khin J, Landers TJ, Lawrence G, Ludbrook MR, Bishop CD 2021. Ecological Integrity of Forests in Tāmaki Makaurau / Auckland 2009-2019. State of environment reporting No. 2021/01. Auckland, Auckland Council. 97 p.

Groenteman R 2022. Environmental weeds in the spotlight. Manaaki Whenua – Landcare Research: Weed Biocontrol newsletter https://www.landcareresearch.co.nz/publications/weed-biocontrol/weed-biocontrol-articles/environmental-weeds-in-the-spotlight/ (accessed 30 May 2023).

Haufler CH, Pryer KM, Schuettpelz E, Sessa EB, Farrar DR, Moran R, Schneller JJ, Watkins JE Jr, Windham MD 2016. Sex and the single gametophyte: Revising the homosporous vascular plant life cycle in light of contemporary research. BioScience 66(11): 928–937.

Heenan PB, de Lange PJ, Cameron EK, Ogle CC, Champion PD 2004. Checklist of dicotyledons and pteridophytes naturalised or casual in New Zealand: Additional records 2001-2003. New Zealand Journal of Botany 42: 797–814.

Horrocks M 2004. Polynesian plant subsistence in prehistoric New Zealand: a summary of the microfossil evidence. New Zealand Journal of Ecology 42: 321–334.

Hoshizaki BJ 1972. Morphology and phylogeny of *Platycerium* species. Biotropica 4(2): 93–117.

Hughes RH 1984. *Platycerium bifurcatum* in the wild and in cultivation. Fiddlehead Forum: Bulletin of I American Fern Society 11(4): 17–21.

Hulme PE 2020. Plant invasions in New Zealand: global lessons in prevention, eradication and control. Biological Invasions 22(5): 1539–1562.

Innes J, Kelly C, Fitzgerald N, Warnock M, Waas J 2018. Detection of wild house mice and other small mammals up trees and on the ground in New Zealand native forest. New Zealand Journal of Zoology 45(3): 227–237.

Jones EJ, Kraaij T, Guerbois C, Moodley D 2020. An assessment of the invasion status of terrestrial alien ferns (Polypodiophyta) in South Africa. South African Journal of Botany 131: 64–73.

Jones EJ, Kraaij T, Fritz H, Moodley D 2019. A global assessment of terrestrial alien ferns (Polypodiophyta): species' traits as drivers of naturalisation and invasion. Biological Invasions 21(3): 861–873.

Kirby C 2014. The last uninvaded frontier? [Blog] The New Zealand Epiphyte Network. Blog. https://www.nzepiphytenetwork.org/blog/the-last-uninvaded-frontier (Accessed 22 March 2023)

Kovářová M, Pyszko P, Plášek V 2022. How does the pH of tree bark change with the presence of the epiphytic bryophytes from the family Orthotrichaceae in the interaction with trunk inclination? Plants 11(1): 63.

Kreier H-P, Schneider H 2006. Phylogeny and biogeography of the staghorn fern genus *Platycerium* (Polypodiaceae, Polypodiidae). American Journal of Botany 93(2): 217–225.

Lyttleton Times 1868. Lyttletone Horticultural Show. Lyttleton Times, Christchurch, 1868, XXX/2474, 26 November 1868, https://paperspast.natlib.govt.nz/newspapers/LT18681126.2.13 (Accessed 15 August 2023)

Lyttleton Times 1871. Christchurch Horticultural Society. Lyttletone Times, Christchurch, 1871, XXXV/3157, 24 February 1871, https://paperspast.natlib.govt.nz/newspapers/LT18710224.2.13 (Accessed 15 August 2023)

McAlpine KG, Lamoureaux SL, Westbrooke I 2015. Ecological impacts of ground cover weeds in New Zealand lowland forests. New Zealand Journal of Ecology 39(1): 50–60.

McGlone M, Bourdôt G, Byrom A, Clout M, Goldson S, Nelson W, Popay A, Suckling M, Templeton M 2014. Challenges for pest management in New Zealand. Emerging Issues No. March 2014. Wellington, The Royal Society of New Zealand | Te Apārangi. 15 p.

McGlone MS, Richardson SJ, Jordan GJ 2010. Comparative biogeography of New Zealand trees: Species richness, height, leaf traits and range sizes. New Zealand Journal of Ecology 34(1): 137–151.

Nzflora 2023. *Platycerium bifurcatum* (Cav.) C.Chr. New Zealand Flora https://www.nzflora.info/factsheet/taxon/Platycerium-bifurcatum.html (accessed 1 May 2023).
NZPCN 2023. FAQs – New Zealand plants. New Zealand Plant Conservation Network https://www.nzpcn.org.nz/help/faq/new-zealand-plants/ (Accessed 1 May 2023)
New Zealand Graphic and Ladies' Journal 1904. Our illustrations. New Zealand Graphic, XXXII/XI, 12 March 1904, https://paperspast.natlib.govt.nz/periodicals/NZGRAP19040312.2.43 (Accessed 15 August 2023)
Otago Daily Times 1903. Dunedin Horticultural Society – annual show. Otago Daily Times, 1903, 12615, 19 March 1903, https://paperspast.natlib.govt.nz/newspapers/ODT19030319.2.17 (Accessed 15 August 2023)
Peck JH, Peck CJ, Farrar DR 1990. Influences of life history attributes on formation of local and distant fern populations. American Fern Journal 80(4): 126–142.
Pemberton RW 2003. The common staghorn, *Platycerium bifurcatum*, naturalises in southern Florida. American Fern Journal 93(4): 203–206.
Planterina Holdings LLC 2023. Staghorn fern. Planterina® https://planterina.com/blogs/indoor-plant-care/staghorn-fern (Accessed 30 May 2023).
R Core Team 2015. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
Sheppard CS, Burns BR, Stanley MC 2016. Future-proofing weed management for the effects of climate change: is New Zealand underestimating the risk of increased plant invasions? New Zealand Journal of Ecology 40(3): 398–405.
Solikin S 2014. *Platycerium bifurcatum* (Cav.) C.Chr. di Kebun Raya Purwodadi. Proceeding Biology Education Conference: Biology, Science, Environmental, and Learning 11(1): 330–335.
Space JC, Flynn T 2002. Report to the Government of Samoa on invasive plant species of environmental concern. Honolulu, Hawai'I, USDA Forest Service. 80 p.
Spier L, van Dobben H, van Dort K 2010. Is bark pH more important than tree species in determining the composition of nitrophytic or acidophytic lichen floras? Environmental Pollution 158(12): 3607–3611.
Sullivan JJ, Timmins SM, Williams PA 2005. Movement of exotic plants into coastal native forests from gardens in northern New Zealand. New Zealand Journal of Ecology 29(1): 1–10.
The Press 1867. Horticultural exhibition. The Press, Christchurch, XI/1323, 2 February 1867, https://paperspast.natlib.govt.nz/newspapers/CHP18670202.2.15 (Accessed 15 August 2023)
The Press 1870. Christchurch Horticultural Society. The Press, Christchurch, 1870, XVII/2383, 17 December 1870, https://paperspast.natlib.govt.nz/newspapers/CHP18701217.2.10 (Accessed 15 August 2023)
The Sun (Auckland) 1929. The stag's horn fern. The Sun, Auckland, III/696, 22 June 1929, https://paperspast.natlib.govt.nz/newspapers/SUNAK19290622.2.200.3 (Accessed 15 August 2023)
Waikato Times 1923. Lovers of a garden. Waikato Times, Hamilton, 96/15874, 21 Decemvber 1923, https://paperspast.natlib.govt.nz/newspapers/WT19231221.2.14.2 (Accessed 15 August 2023)
Wilson EH 1927. Plant hunting v. 1. Africa, south and central Australia and New Zealand. Boston, Stratford Co. 418 p.
Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH 2008. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proceedings of the National Academy of Sciences of the United States of America 105(22): 7676–7680.
Wilson KA 1996. Alien ferns in Hawai'i. Pacific Science 50(2): 127–141.
Wu J 2023. Auckland urban epiphytes – a nexus of invasion. Unpublished MSc thesis. University of Auckland, Auckland, New Zealand.

Received: 30 May 2023; accepted: 23 August 2023
Editorial board member: David Wardle

Supplementary material

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

Appendix S1. Location data of *Platycerium bifurcatum* individuals observed during this study.

The New Zealand Journal of Ecology provides supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.