

Article

Tree Ferns Augment Native Plant Richness and Influence Composition in Urban Plant Communities

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Abstract

Tree ferns are ubiquitous in New Zealand forests, but there is limited knowledge of their role in urban plant communities and potential use in restoration. We assessed sixteen sites by measuring 200 m² plots to investigate how tree ferns influence vascular plant composition in Hamilton, North Island, New Zealand. The sixteen plots were assigned to four site type combinations based on restoration status (restored or unrestored) and tree fern presence, each with four plots. Average native plant species richness was higher at sites with tree ferns (36 ± 16 ; $S = 68$) than at sites without (19 ± 14 ; $S = 41$), with more diverse ground fern and epiphyte assemblages. Higher native plant richness at restored sites (34 ± 18 ; $S = 62$) compared to unrestored sites (20 ± 14 , $S = 44$) was partially attributed to increased plant abundances. Multivariate analyses revealed differences in plant community composition among our site types. Angiosperms and conifers were less prevalent in plots with tree ferns, suggesting competitive relationships among these groups. However, tree ferns were associated with some shade-tolerant trees, such as *Schefflera digitata* J.R.Forst. & G.Forst. Indicator species of sites with tree ferns were mainly ground ferns and epiphytes (e.g., *Blechnum parrisiae* Christenh. and *Trichomanes venosum* R.Br.), whereas species with high fidelity to sites without tree ferns were pioneer trees and shrubs (e.g., *Pittosporum eugenioides* A.Cunn.). Community structure analyses revealed that total basal areas were highest at unrestored sites with tree ferns, but restored sites exhibited more diverse tree communities. Environmental predictors that correlated significantly with the compositional differences among our site types were tree fern basal area and restoration age. Our results highlight the need to reconsider the potential of tree ferns in current restoration practice. Tree ferns were found to augment native plant diversity in our study, indicating their potential to enhance urban ecological restoration projects in New Zealand.

Keywords: community assembly; ecological restoration; urban ecology; composition; vascular plants; pioneer species; epiphytes; life forms; diversity; New Zealand



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1. Introduction

Forests support a significant portion of global biodiversity and provide myriad ecosystem services. However, global forest loss is still high, mainly driven by agricultural and urban development [1,2]. Urban expansion places significant pressure on biodiversity via habitat loss and modification [3], but urban ecological restoration presents a unique nature-based solution to combat biodiversity loss and climate change [4,5]. As the number of urban restoration projects rises internationally [6], there is a growing need to contribute to current knowledge of urban plant community composition and assembly. Pioneer species

play a critical role in ecological succession and community assembly, influencing the successional pathway and “climax” community [7,8]. Early-arriving plants also impact the functional diversity of ecosystems [9] and the number of colonising species via community competition [10]. Understanding how pioneers influence community composition is vital for successful restoration, allowing restoration practitioners to mimic natural succession and assist the recovery of disturbed ecosystems to support a fuller assemblage of species.

In New Zealand, restoration practitioners concentrate on restoring pioneer trees and shrubs [11], which we refer to as light-demanding angiosperm and conifer species first planted at restoration projects. In contrast, we are unaware of any urban restoration projects where tree ferns have been planted, despite also being important pioneers of conifer-broadleaved forests [12]. Tree ferns can act as ecological filters, either inhibiting or facilitating the regeneration of other plants [13–15]. When forming extensive thickets, tree ferns may arrest succession, restricting the arrival of pioneer angiosperms and conifers via shading effects and slow-decomposing fronds. For example, tree ferns suppressed podocarp regeneration in exotic [16] and indigenous forests [17–20]. A stand of *Cyathea dealbata* (G.Forst.) Sw. also restricted angiosperm establishment in secondary forests on the Coromandel Peninsula [21].

Previous research indicates that tree ferns can also accelerate successional processes [22]. For example, they contribute to soil development, provide slope stabilisation and are excellent phorophytes [23–25]. Tree ferns enhance habitat heterogeneity, influencing nutrient, light and water cycles via their megaphylls and providing substrate conducive to epiphyte establishment [26]. Furthermore, tree ferns can provide an important regeneration niche for angiosperms, mediating competition with conifers [27]. A study in the Waitutu Ecological District found that 60% of mature *Pterophylla racemosa* (L.f.) Pilon & H.C.Hopkins (a native angiosperm tree) regenerated epiphytically on tree ferns [13]. Tree fern stands may also provide a more suitable habitat for shade-tolerant species than pioneer trees. For example, forest dominated by *Cyathea medullaris* G.Forst.) Sw. supported more shade-tolerant species than *Kunzea ericoides* s.l. (A.Rich.) forest [28]. Furthermore, extant tree ferns may advance restoration by decades by providing a native canopy (a primary goal in ecological restoration) from the outset of projects. Common pioneer species planted in restoration projects, such as *Leptospermum scoparium* J.R.Forst. & G.Forst. and *Kunzea ericoides*, may take twenty years to reach a height of 7 m [29].

Research on community assembly and successional pathways following tree ferns is scarce. However, gullies and topographic depressions with early-colonising tree ferns (e.g., *Dicksonia squarrosa* (G.Forst.) Sw. and *Cyathea medullaris*) may encourage broadleaved scrub 35–50 years after disturbance, *Beilschmiedia tawa* (A.Cunn.) Benth. & Hook.f. ex Kirk forest after 150–350 years and *Metrosideros robusta* A.Cunn.–*Dacrydium cupressinum* Sol. ex G.Forst.–*B. tawa* forest after 400 years [30]. In Hamilton urban environments, successional pathways have diverged from natural forest trajectories due to the range of anthropogenic disturbances that influence plant communities. Images show that grey willow-dominated forest containing *Dicksonia squarrosa* established in some gullies more than 20 years after livestock grazing ceased when land was subdivided for housing development [31]. Although tree ferns form important pioneer communities of conifer-broadleaved forests in New Zealand, there is limited information on how these species influence urban plant communities.

We present the results from one of the first studies on urban tree fern communities in New Zealand; most research on tree ferns has focused on non-urban forests after natural, rather than anthropogenic disturbance. The aim of this study was to investigate how tree ferns influence urban plant communities and identify environmental variables contributing to community composition. We tested three hypotheses: (1) tree fern presence significantly

affects vascular plant community composition at sites not actively restored by augmenting ground fern and epiphyte richness, (2) actively restored sites support richer, more abundant pioneer tree and shrub assemblages and (3) tree fern basal area and restoration age are important environmental predictors of compositional differences among our site types. Better understanding how tree ferns impact diversity and composition in urban plant communities will help guide ecological restoration activities.

2. Materials and Methods

2.1. Study Area

Indigenous vegetation cover is low in New Zealand's major urban centres, ranging from <1 to 8.9% [32]. Urban forests support novel plant communities with a high prevalence of exotic species [33]. Research on restoring urban forests has focused on forest remnants or reconstructing native ecosystems using landforms to guide plantings [34,35]. With a focus on planting pioneer trees, there has been little research on existing pioneer tree ferns. Practitioners have also overlooked tree ferns and the native species they support; the blanket clearance of exotic trees, a common approach, is unfavourable to existing native plants, including tree ferns [36].

Hamilton is a small city (approximately 11,000 ha) located in the central North Island, New Zealand (37°46'59.99" S, 175°16'59.99" E). New Zealand has been identified as one of 25 world biodiversity hotspots for conservation priorities [37]. Hamilton lies within the Hamilton Ecological District [38]. Hamilton has a temperate oceanic climate with a mean annual temperature of 13.7 °C and a mean annual precipitation of 1190 mm [39]. There is approximately 267 ha (2.5%) of native-dominant vegetation in Hamilton (HCC unpublished database). Hamilton's natural vegetation is concentrated in gullies that form intricate networks throughout the city. The gullies formed 15,000 years ago via spring sapping when the Waikato River changed course, undermining banks, trapping sediment and creating a network of streams. Before human arrival, gully floors were dominated by semi-swamp species like *Dacrycarpus dacrydioides* (A.Rich.) de Laub. (kahikatea), *Laurelia novae-zelandiae* A.Cunn. (pukatea) and *Syzygium maire* (A.Cunn.) Sykes & Garn.-Jones (waiwaka) [34]. As rural land in Hamilton was converted to urban subdivisions, grey willow (*Salix cinerea*) rapidly became the dominant tree in the gullies. Compared to small, drained kahikatea remnants in Hamilton, the gullies, with their developed canopy, higher humidity and abundant tree ferns, may support more diverse native understory communities [40]. Hamilton's gullies can also support rich assemblages of locally uncommon life forms, including epiphytes [41].

2.2. Site Selection

After an extensive survey of gullies and reserves in Hamilton, sixteen sites were selected (Figure 1). We adopted a fully crossed factorial design to investigate how tree fern presence influences urban plant communities while considering the impact of active plantings on these communities using restoration status. Our site types consisted of four categories: restored sites with tree ferns (n = 4), unrestored sites with tree ferns (n = 4), restored sites without tree ferns (n = 4) and unrestored sites without tree ferns (n = 4). Restored sites had been planted with native trees and shrubs (native tree basal area > 7 m² ha⁻¹), and unrestored sites had not been planted (<3 m² ha⁻¹). Sites with tree ferns had at least 12 individuals in a plot, and those without had three or fewer (see Figure 2 for site type examples). The thresholds used to determine site type were adopted as feasible targets for the study sites, enabling a comparison between sites with and without tree ferns.

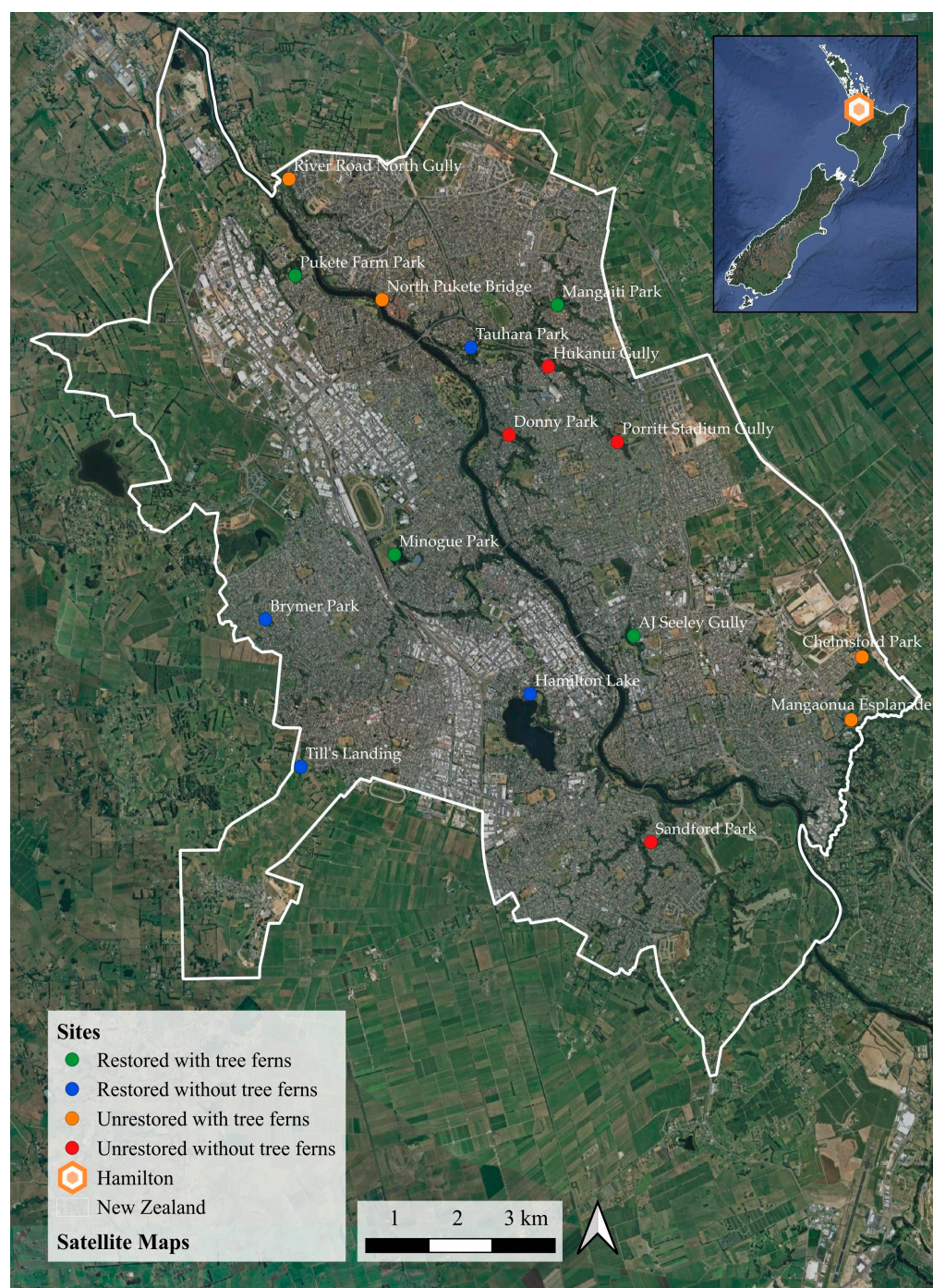


Figure 1. Site locations in Hamilton, North Island, New Zealand. Each dot represents a site where one $20 \times 10 \text{ m}^2$ vegetation plot was assessed, and the colour denotes the site type (i.e., green dots are restored sites with tree ferns, blue dots are restored sites without tree ferns, orange dots are unrestored sites with tree ferns and red dots are unrestored sites without tree ferns). A map of New Zealand is also provided, indicating the study location (Hamilton), near the centre of the North Island.



Figure 2. Example sites of the four site types based on restoration status (restored, unrestored) and the presence of tree ferns (with, without).

Restoration age (i.e., the time since native plantings began) guided site selection and was sourced from an unpublished Hamilton City Council restoration database and verified using tree cores [42] (see Table S1, Supplementary Materials). The tree fern basal areas at sites with tree ferns (dominated by *Dicksonia squarrosa*) were similar to those recorded in younger (<80 years) podocarp–broadleaf forests on central North Island [19]. The soil types at our sites ranged from Kirikiriroa gritty silt loam, Te Kowhai silt loam, Tamahana silt loam, Kainui silt loam and Waikato loamy sand to Hamilton clay loam and Kaipaki peaty loam (Manaaki Whenua unpublished database). All four site types exhibited the two major soil types (Kirikiriroa gritty silt loam and Tamahana silt loam).

2.3. Vegetation Survey

A single vegetation plot ($20 \times 10 \text{ m}^2$) was measured at each site, following a method developed by the People, Cities and Nature (PCaN) research programme and used in establishing a permanent plot network of 97 plots in nine cities across New Zealand [43]. Four permanent vegetation plots (200 m^2) were selected from the PCaN plot network in Hamilton ($n = 9$) that met the restored sites without tree ferns' site type requirements. The remaining twelve sites that met the requirements of the other three site types (i.e., not in the PCaN plot network) were selected separately; specific plot locations were identified using a random number generator. Our plots were half the area of the nationally developed forest methodology [44] because of the limited patch size and extent of vegetation in the urban context (Figure S1, Supplementary Materials).

Each plot was split into eight 5 m^2 subplots, and measurements were obtained for ground cover, ground ferns, woody plants (trees and shrubs), tree ferns and epiphytes. The ground cover (%) per subplot was estimated visually using standard categories (i.e., herbaceous cover, leaf litter and sticks, moss and bare ground). Ground ferns were counted per subplot. For woody species, data were collected separately for seedlings (<1.35 m tall), saplings (>1.35 m tall but <2.5 cm diameter at breast height, DBH) and trees (woody species > 2.5 cm DBH). Tree ferns were counted per subplot; we only recorded tree fern diameters for individuals with a DBH greater than 2.5 cm. Vascular epiphyte

measurements included abundance (count) and host species. The nomenclature follows the Flora of New Zealand [45].

In addition, variables that could influence the study communities were recorded, specifically canopy cover (using the %Cover CanopySurveying application), slope (using a SUUNTO PM-5 clinometer, Vantaa, Finland), canopy height (with a Hagl f Vertex IV Hypsometer, L ngsele, Sweden) and geographical coordinates. A tree core from the largest individual was collected from each plot to estimate the maximum age and verify previously documented restoration ages (Table S1, Supplementary Materials). Distance from the patch edge (i.e., between the plot and vegetation margin) was determined using the Near geoprocessing tool in ArcGIS Pro (a geographic information system).

2.4. Data Analysis

We compared compositional differences among our four site types (i.e., unrestored sites with tree ferns, unrestored sites without tree ferns, restored sites with tree ferns and restored sites without tree ferns) and investigated environmental variables influencing these differences using a range of statistical approaches. Data was analysed and visualised in R version 4.2.2 [46]. Unless specified, all multivariate analyses used the “vegan” R package (version 2.7-1) [47].

2.4.1. Community Analysis

We investigated the influence of our site types on plant richness to test our first two hypotheses (i.e., tree ferns augment native plant richness, and restored sites hold more speciose and diverse plant communities). To account for differences in plant abundances, we estimated rarefied species richness for each plot and plant group (i.e., seedlings, saplings, trees, ground ferns and epiphytes) using a sample-size-based rarefaction and extrapolation (R/E) sampling curve approach with the “iNEXT” (version 3.0.0) R package [48]. Rarefaction curves were extrapolated to a higher number of individual plants for total native species richness ($n = 200$) than for exotic richness and individual plant groups ($n = 50$). The different approaches were explained by the lower abundances of the latter groups, requiring a smaller number of individuals to standardise richness (Figure A1).

We then fitted generalised linear models (GLMs) with restoration age as a covariate to test the influence of tree fern presence and restoration status on species abundances and richness of different plant groups (i.e., native and exotic plant species and individual plant groups, including seedlings, saplings, trees, ground ferns and epiphytes). We compared GLM results using raw (i.e., unrarefied) and rarefied species richness, but we present results for the latter, as rarefaction accounts for the influence of plant abundances on richness responses [48]. The GLMs using count data responses were fitted with a log link function, assuming a Poisson distribution. We tested the multivariate models for multicollinearity using the variance inflation factor (VIF); all models achieved acceptable VIF values below 5. We compared models with and without the interaction term using a likelihood ratio test to determine whether there were interactive effects between restoration status and tree fern presence. Where there was no statistically significant influence of the interaction, we present the additive model results. Post hoc comparisons were tested using a least-squares means approach with Tukey’s correction for multiplicity via the “lsmeans” package in R [49]. In addition to key model statistics provided in the written results, we present summary tables in the results with the 95% confidence interval for the parameter estimates of the GLMs and post hoc tests.

To assess how tree fern presence and restoration status influence plant community composition, we used a permutational multivariate analysis of variance (PERMANOVA) with abundance data for native and exotic species, combined and native species alone. The PERMANOVA tests were performed using the “adonis2” function in the “vegan” R package [47]. Community composition data were first Hellinger-transformed to simultaneously minimise the effects of vastly different total abundances and account for rare species [50]. The transformed community data using the Bray–Curtis dissimilarity was then analysed with PERMANOVA to test whether plant community composition differed among our four site types [51]. Each PERMANOVA model included restoration age as a covariate. To determine which plant species were influential in the PERMANOVA results, we used the “indicspecies” (version 1.8.0) R package to identify indicator species with high fidelity to our site types [52]. A nonmetric multidimensional scaling (NMDS) ordination using the “metaMDS” function was used to visualise plant communities in each site type and help interpret the PERMANOVA results. Convex hulls were drawn around the four site types, and indicator species and the ten most abundant species (i.e., species ranked by dominance) were plotted using their axes scores.

We used basal areas (as an indicator of biomass) to test our first two hypotheses further regarding the influence of tree fern presence and restoration status on vascular plant communities. We fitted four GLMs (each assuming a Gaussian distribution) to investigate differences in total, native tree, exotic tree and tree fern basal areas among the site types with restoration age as a covariate. Model predictors in the GLMs had acceptable variance inflation factor (VIF) values < 5 . Post hoc differences were tested using a least-squares means approach with Tukey’s correction for multiplicity. We also tested compositional differences in species basal areas among the site types using PERMANOVA, but we did not present the results, as they reiterate the same compositional differences among our site types found using species abundances.

2.4.2. Environmental Variable Analysis

To test our third hypothesis, we investigated the influence of potential environmental predictors on plant community responses, including species richness and community composition. Six GLMs were fitted to identify potential environmental predictors of richness for total native species and each plant group (i.e., seedlings, saplings, trees, ground ferns and epiphytes) using a log link function and assuming a Poisson distribution for count data. The ten environmental predictors we considered were average slope, canopy cover, restoration age, maximum tree age, maximum tree height, distance to the patch edge, and the total plant basal area, as well as the basal area of tree ferns, native trees and exotic trees. We assessed the normality of environmental predictors using Shapiro tests and log-transformed predictors to reduce skewness. Environmental predictors were then standardised (i.e., centred on the mean and scaled to unit variance) using the “decostand” function in the “vegan” R package. Rarefied richness integers were used for all models to account for differences in plant abundances across site types. The “step” R function was used to forward select important environmental predictors (from our ten predictors) of our univariate responses for each model.

To consider potential environmental and spatial predictors of overall plant community composition and account for potential spatial autocorrelation, a distance-based redundancy analysis (dbRDA) using the Bray–Curtis dissimilarity [53] was conducted on the Hellinger-transformed community data. The same ten log-transformed and standardised environmental predictors used for the univariate GLMs were considered for the dbRDA.

In our initial model fitting for the dbRDA, we also considered spatial structuring of plant communities (e.g., distance–decay relationships). The spatial structuring of plant community data using geographic coordinates for sites was assessed using a principal coordinates of neighbour matrices (PCNM) approach [54]. PCNM descriptors (or axes) may help describe processes structuring communities at different spatial scales [55]. PCNM axes were generated from site coordinates using the “pcnm” R function in the “vegan” package. The PCNM axes were used in the initial model selection procedure for the dbRDA, but none were selected, and they were not considered further.

To avoid overfitting the dbRDA model and select only influential predictors explaining variation in plant community composition, we used a forward stepwise procedure using the “ordistep” function [56]. Two predictors were selected for the final dbRDA model: tree fern basal area and restoration age. Variation partitioning was then undertaken to assess the relative contribution of tree fern basal area and restoration age to variation in community composition (Figure S2, Supplementary Materials). The significance of each independent variation component was permutation-tested using 1000 randomisations [57]. We used the “capscale” (dbRDA) and “varpart” (variation partitioning) functions for these constrained multivariate analyses.

3. Results

3.1. Plant Abundances and Richness

More than 6000 individuals of 155 native vascular plant species were recorded across 16 sites (Table 1). The generalised linear model (GLM) results showed significant differences in plant abundances and species richness with tree fern presence and restoration status (Table 2). Native plant abundances were significantly affected by the interaction between tree fern presence and restoration status ($F_{1,11} = 12.0, p < 0.01$). Post hoc results revealed that native plant abundances were higher at restored sites without tree ferns when compared to their unrestored equivalents ($z = 2.7, p < 0.01$), but unrestored sites with tree ferns exhibited higher native abundances than the restored sites ($z = -9.7, p < 0.001$). Restored sites without tree ferns presented higher native abundances than those with tree ferns ($z = 6.3, p < 0.001$), whereas the opposite was observed at unrestored sites with tree ferns, which showed higher abundances than unrestored sites without tree ferns ($z = -35.6, p < 0.001$).

Table 1. Mean ($\pm$ standard deviation) native, exotic and total plant abundances, richness and rarefied richness at the four site types based on restoration status (restored, unrestored) and tree fern presence (with, without). The mean total (i.e., tree fern, native and exotic tree) basal areas (m^2/ha) per site type are also presented.

Group	Variable	Unrestored with Mean $\pm$ SD	Unrestored Without Mean $\pm$ SD	Restored with Mean $\pm$ SD	Restored Without Mean $\pm$ SD
Native	Abundance	659.5 $\pm$ 449.3	61.5 $\pm$ 50.0	295.0 $\pm$ 82.0	351.8 $\pm$ 186.9
	Richness	32.8 $\pm$ 3.8	8.5 $\pm$ 5.8	38.5 $\pm$ 23.3	29.5 $\pm$ 12.5
	Rarefied richness	20.2 $\pm$ 1.4	6.7 $\pm$ 5.0	20.0 $\pm$ 4.5	16.1 $\pm$ 1.1
Exotic	Abundance	40.8 $\pm$ 25.0	132.3 $\pm$ 125.8	16.5 $\pm$ 25.2	54.8 $\pm$ 49.3
	Richness	7.0 $\pm$ 1.4	7.3 $\pm$ 4.0	3.5 $\pm$ 1.7	8.0 $\pm$ 3.4
	Rarefied richness	4.4 $\pm$ 2.4	4.6 $\pm$ 2.9	2.1 $\pm$ 1.6	6.5 $\pm$ 3.4
Total	Abundance	700.3 $\pm$ 465.9	193.8 $\pm$ 169.3	311.5 $\pm$ 66.4	406.5 $\pm$ 195.2
	Richness	39.8 $\pm$ 5.0	15.8 $\pm$ 7.9	42.0 $\pm$ 22.7	37.5 $\pm$ 14.0
	Rarefied richness	24.3 $\pm$ 2.3	13.0 $\pm$ 2.8	22.5 $\pm$ 5.2	22.1 $\pm$ 3.8
	Basal area	25.7 $\pm$ 12.2	9.0 $\pm$ 6.8	18.5 $\pm$ 3.3	18.4 $\pm$ 3.4

Table 2. Generalised linear model results testing the effect of tree fern presence and restoration status on total native abundances and rarefied species richness, as well as the abundance and rarefied richness of seedlings, ground ferns and epiphytes. Incidence rate ratios with 95% confidence intervals (CI) are provided. Statistically significant p -values at $\alpha = 0.05$ are in boldface. See Supplementary Materials, Table S2, for GLM results concerning total exotic plants, native saplings and trees abundances and richness.

Model	Predictors	Incidence Rate Ratio	95% CI	p -Value
Total native abundances	(Intercept)	294.83	119.39–679.37	<0.001
	Tree ferns [Yes]	0.76	0.28–1.93	0.571
	Status [Unrestored]	0.42	0.01–14.98	0.633
	Restoration age [$\log(x) + 1$]	1.49	0.35–6.51	0.584
	Tree ferns [Yes] $\times$ Status [Unrestored]	14.12	2.92–108.85	0.003
Rarefied native species richness (n = 200)	(Intercept)	13.10	8.65–19.45	<0.001
	Tree ferns [Yes]	1.10	0.71–1.71	0.663
	Status [Unrestored]	1.18	0.27–5.17	0.825
	Restoration age [$\log(x) + 1$]	1.60	0.87–2.97	0.133
	Tree ferns [Yes] $\times$ Status [Unrestored]	2.72	1.38–5.55	0.005
Rarefied seedling richness (n = 50)	(Intercept)	4.53	2.46–8.00	<0.001
	Tree ferns [Yes]	0.47	0.22–0.93	0.037
	Status [Unrestored]	2.72	0.25–33.83	0.420
	Restoration age [$\log(x) + 1$]	3.00	1.10–8.78	0.036
	Tree ferns [Yes] $\times$ Status [Unrestored]	3.89	1.26–13.07	0.021
Ground fern abundances	(Intercept)	12.67	2.26–49.91	0.001
	Tree ferns [Yes]	7.45	2.47–33.96	0.002
	Status [Unrestored]	0.15	0.00–8.77	0.368
	Restoration age [$\log(x) + 1$]	0.38	0.05–2.02	0.288
Rarefied ground fern richness (n = 50)	(Intercept)	0.99	0.41–2.14	0.974
	Tree ferns [Yes]	3.98	2.24–7.60	<0.001
	Status [Unrestored]	1.42	0.12–16.66	0.776
	Restoration age [$\log_1 p$]	0.95	0.34–2.54	0.922
Native epiphyte abundances	(Intercept)	15.28	0.03–493.91	0.211
	Tree ferns [Yes]	6.77	0.80–401.85	0.156
	Status [Unrestored]	3.35	0.00–22.29 $\times 10^6$	0.850
	Restoration age [$\log(x) + 1$]	0.89	0.00–252.60	0.963
Rarefied native epiphyte richness (n = 50)	(Intercept)	0.62	0.18–1.77	0.411
	Tree ferns [Yes]	5.40	2.42–14.23	<0.001
	Status [Unrestored]	10.21	0.59–229.80	0.123
	Restoration age [$\log(x) + 1$]	2.25	0.72–7.26	0.163

Native plant abundances appeared to partially affect native species richness, which was higher at restored sites, whether tree ferns were present ($z = -5.1$, $p < 0.001$) or absent ($z = -3.2$, $p < 0.01$). However, after accounting for differences in native plant abundances through rarefaction, the GLM revealed that the interaction between tree fern presence and restoration status had a significant effect on plant richness ($F_{1,11} = 8.4$, $p < 0.05$; see Figure 3). Tree fern presence positively influenced rarefied native plant richness at unrestored sites ($z = -4.0$, $p < 0.001$), but this influence was not statistically significant at restored sites ($z = -1.0$, $p = 0.3$). In contrast, restoration status positively affected native species richness at sites without tree ferns ($z = 2.9$, $p < 0.01$), but it did not have a significant influence at sites without tree ferns ($z = -0.04$, $p = 1.0$).

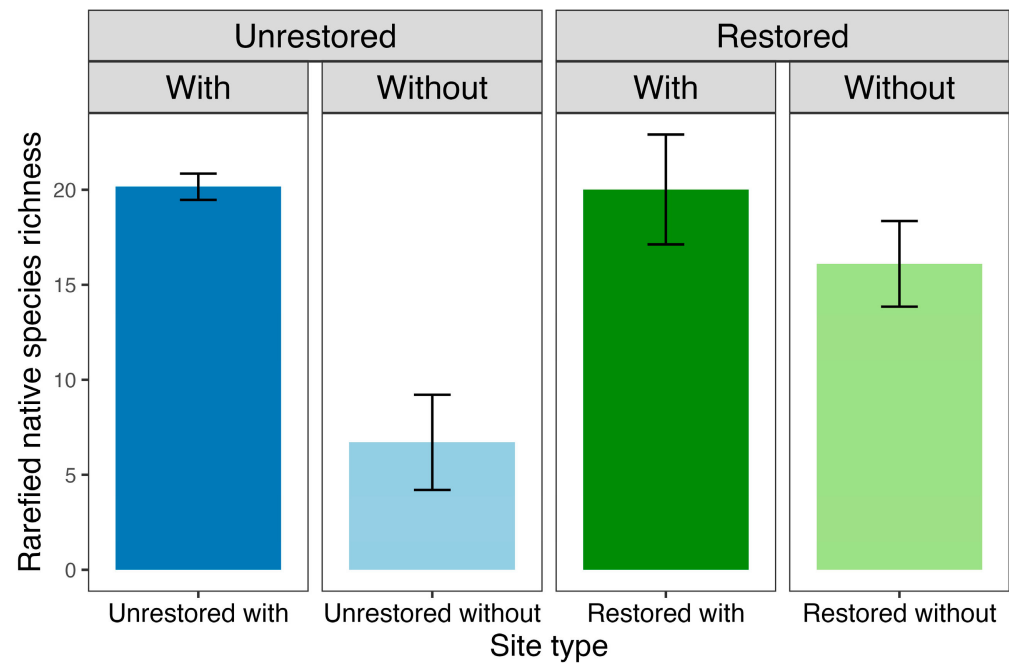


Figure 3. Mean rarefied native vascular plant species richness for the four site types based on restoration status (restored, unrestored) and the presence of tree ferns (with, without). Error bars represent one standard error.

Exotic plant abundances were significantly lower at sites with tree ferns ($F_{1,12} = 6.6$, $p < 0.05$) but did not vary with restoration status ($F_{1,12} = 2.4$, $p = 0.2$). Furthermore, rarefied exotic species richness was not significantly influenced by tree fern presence ($F_{1,12} = 2.1$, $p = 0.2$) or restoration status ($F_{1,12} = 0.4$, $p = 0.5$).

The abundances and species richness of native plant groups differed across site types (Tables 2 and 3). Seedling abundances were not significantly influenced by tree fern presence ($F_{1,12} = 0.2$, $p = 0.7$) or restoration status ($F_{1,12} = 0.02$, $p = 0.9$). Rarefied native seedling richness was significantly influenced by the interaction between tree fern presence and restoration status ($F_{1,11} = 5.6$, $p < 0.05$). Post hoc results showed that tree ferns negatively affected rarefied seedling richness restored sites ($z = 2.1$, $p < 0.05$) but had no significant effect at unrestored sites ($z = -1.3$, $p = 0.2$). Furthermore, restoration status did not significantly influence rarefied seedling richness when tree ferns were present ($z = -1.7$, $p = 0.1$) or absent ($z = -1.1$, $p = 0.3$).

Table 3. Mean ($\pm$ standard deviation) native species abundance, richness and rarefied richness for each plant group and site type. Our plant groups were tree ferns, seedlings, saplings, trees, ground ferns and epiphytes. Site types were based on restoration status (restored, unrestored) and tree fern presence (with, without). The mean tree fern basal areas ($\text{m}^2 \text{ha}^{-1}$) per site type are also presented.

Plant Group	Variable	Unrestored with Mean $\pm$ SD	Unrestored Without Mean $\pm$ SD	Restored with Mean $\pm$ SD	Restored Without Mean $\pm$ SD
Tree ferns	Abundance	68.8 $\pm$ 33.9	0.8 $\pm$ 1.5	25.0 $\pm$ 12.1	0.5 $\pm$ 1.0
	Richness	2.3 $\pm$ 1.3	0.3 $\pm$ 0.5	2.3 $\pm$ 1.0	0.3 $\pm$ 0.5
	Rarefied richness	2.1 $\pm$ 1.3	1 $\pm$ 0.0	2.3 $\pm$ 1.0	1 $\pm$ 0.0
	Basal area	21.1 $\pm$ 10.5	0.2 $\pm$ 0.4	6.1 $\pm$ 1.5	0.0 $\pm$ 0.0
Seedlings	Abundance	24.3 $\pm$ 4.0	7.3 $\pm$ 11.3	101.5 $\pm$ 100.9	125.0 $\pm$ 144.7
	Richness	3.5 $\pm$ 1.0	1.3 $\pm$ 1.3	7.8 $\pm$ 6.6	9.3 $\pm$ 5.6
	Rarefied richness	3.2 $\pm$ 1.2	1.8 $\pm$ 1.5	4.9 $\pm$ 3.3	7.4 $\pm$ 3.2

Table 3. Cont.

Plant Group	Variable	Unrestored with Mean $\pm$ SD	Unrestored Without Mean $\pm$ SD	Restored with Mean $\pm$ SD	Restored Without Mean $\pm$ SD
Saplings	Abundance	23.8 $\pm$ 12.2	15.3 $\pm$ 16.5	72.5 $\pm$ 34.4	79.5 $\pm$ 40.3
	Richness	5.3 $\pm$ 3.1	1.5 $\pm$ 0.6	11.0 $\pm$ 8.8	7.8 $\pm$ 2.9
	Rarefied richness	4.5 $\pm$ 2.7	1.5 $\pm$ 0.6	5.5 $\pm$ 3.1	6.0 $\pm$ 1.6
Trees	Abundance	59.8 $\pm$ 21.0	6.0 $\pm$ 7.1	33.3 $\pm$ 9.4	30.5 $\pm$ 9.7
	Richness	4.3 $\pm$ 1.3	2.3 $\pm$ 2.9	8.0 $\pm$ 2.9	9.5 $\pm$ 4.5
	Rarefied richness	3.1 $\pm$ 0.6	2.7 $\pm$ 2.3	6.3 $\pm$ 3.2	7.7 $\pm$ 3.4
Ground ferns	Abundance	75.8 $\pm$ 53.9	14.3 $\pm$ 22.0	58.3 $\pm$ 45.7	4.8 $\pm$ 5.0
	Richness	6.3 $\pm$ 1.0	2.0 $\pm$ 1.4	5.8 $\pm$ 3.8	1.8 $\pm$ 1.5
	Rarefied richness	5.9 $\pm$ 1.5	1.8 $\pm$ 1.3	4.0 $\pm$ 1.4	0.8 $\pm$ 1.0
Epiphytes	Abundance	486.5 $\pm$ 376.0	7.3 $\pm$ 10.4	39.5 $\pm$ 36.2	70.8 $\pm$ 131.1
	Richness	13.5 $\pm$ 3.3	1.5 $\pm$ 1.7	6.0 $\pm$ 5.5	1.3 $\pm$ 1.5
	Rarefied richness	8.6 $\pm$ 1.9	1.0 $\pm$ 1.4	5.5 $\pm$ 5.1	1.4 $\pm$ 1.1

Native sapling abundances were not significantly influenced by tree fern presence ($z = 0.04$, $p = 0.8$) or restoration status ($z = 2.1$, $p = 0.1$). Rarefied native sapling richness was significantly influenced by the interaction between tree fern presence and restoration status ($F_{1,11} = 6.9$, $p < 0.05$). Sapling richness was positively affected by tree fern presence at unrestored sites ($z = -2.4$, $p < 0.05$) but not at restored sites ($z = 0.9$, $p = 0.4$). In comparison, restoration status did not significantly influence rarefied sapling richness when tree ferns were present ($z = -1.5$, $p = 0.2$) or absent ($z = -0.6$, $p = 0.8$).

Native tree abundances (i.e., woody trees excluding tree ferns) were significantly higher at restored sites ($F_{1,12} = 5.6$, $p < 0.05$) but were not affected by tree fern presence ($F_{1,12} = 0.9$, $p = 0.7$). There was no statistically significant difference in rarefied tree species richness with tree fern presence ($F_{1,12} = 0.3$, $p = 0.6$) or restoration status ($F_{1,12} = 0.04$, $p = 0.8$).

Ground fern abundance was significantly higher at sites with tree ferns ($F_{1,12} = 15.1$, $p < 0.01$) but did not differ with restoration status ($F_{1,12} = 1.3$, $p = 0.4$). Likewise, rarefied ground fern richness was strongly positively influenced by tree fern presence ($F_{1,12} = 24.7$, $p < 0.001$) but was not significantly affected by restoration status ($F_{1,12} = 0.01$, $p = 0.8$). While neither tree ferns nor restoration status had a statistically significant effect on epiphyte abundance at the $\alpha = 0.05$ level, tree ferns were associated with increased epiphyte abundance ($F_{1,12} = 3.3$, $p = 0.9$). Furthermore, rarefied native epiphyte richness was significantly higher at sites with tree ferns ($F_{1,12} = 13.2$, $p < 0.001$) but was not affected by restoration status ($F_{1,12} = 2.5$, $p = 0.1$).

3.2. Community Composition

Distinct plant communities were associated with our site types, further supporting our first two hypotheses. Our permutational multivariate analysis of variance (PERMANOVA) models found significant differences in total vascular plant composition (native and exotic species) across all pairwise comparisons except for between restored sites with and without tree ferns (see Figure 4 and Table A1). Native plant composition also differed significantly among five of the six pairwise comparisons across all levels of our factorial design (Table S3, Supplementary Materials).

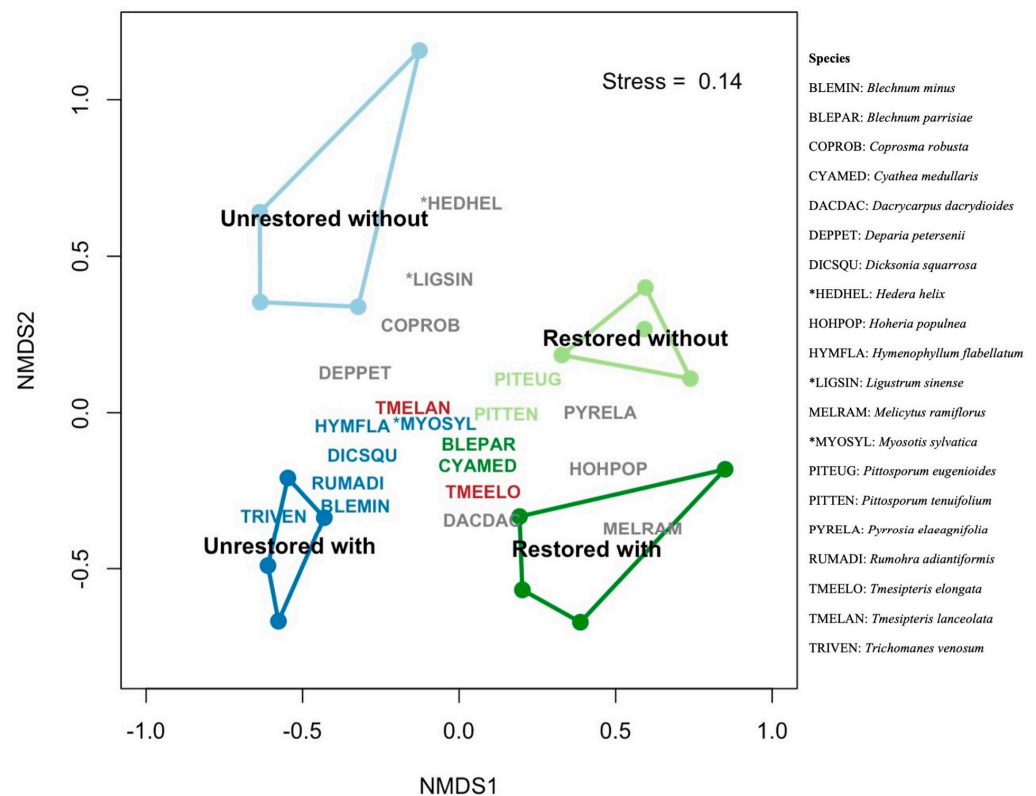


Figure 4. Nonmetric multidimensional scaling (NMDS) ordination of plant community composition by abundances. Convex hulls are drawn around the four site types: restored with tree ferns (dark green), restored without tree ferns (light green), unrestored with tree ferns (dark blue), and unrestored without tree ferns (light blue). The ordination achieved a “fair” stress score of 0.14. The coloured dots represent the sites, and six-letter codes represent the indicator or abundant species (see legend for scientific names). An asterisk denotes an exotic species. Species colours represent indicator species of the site types: restored with tree ferns (dark green), restored without tree ferns (light green) and unrestored with tree ferns (dark blue). The species in grey are eight of the most abundant species, and the species in red (2) represent indicators of unrestored sites with tree ferns that are also abundant species. The ten most abundant species accounted for 62% of the mean relative abundance.

The abundant species (i.e., the ten most dominant species overall) at restored sites were *Dacrycarpus dacrydioides*, *Melicytus ramiflorus* J.R.Forst. & G.Forst., *Hoheria populnea* A.Cunn. and *Pyrrosia elaeagnifolia* (Bory) Hovenkamp. In contrast, the abundant species at sites with tree ferns were *Deparia petersenii* (Kunze) M.Kato, *Tmesipteris lanceolata* P.A.Dang. and *Tmesipteris elongata* P.A.Dang. Three abundant species were associated with sites without tree ferns, a native shrub (*Coprosma robusta* Raoul) and two exotic species (*Hedera helix* L. and *Ligustrum sinense* Lour.).

An indicator species analysis identified 12 species for three site types (Table A2). Unrestored sites with tree ferns were associated with the most indicator species (8), including ground ferns (*Blechnum minus* (R.Br.) Ettingsh.), tree ferns (*Dicksonia squarrosa*), epiphytic ferns (*Tmesipteris elongata*, *T. lanceolata*, *Trichomanes venosum* R.Br., *Rumohra adiantiformis* (G.Forst.) Ching and *Hymenophyllum flabellatum* Labill.) and one exotic herb (*Myosotis sylvatica* Hoffm.). No indicator species were associated with unrestored sites without tree ferns, likely because of their depauperate assemblages. Species with high fidelity to restored sites with tree ferns were *Blechnum parrisiae* Christenh. and *Cyathea medullaris*. In comparison, indicator species of restored sites without tree ferns were *Pittosporum eugenioides* A.Cunn. and *Pittosporum tenuifolium* Sol. ex Gaertn.

3.3. Community Structure

We investigated differences in plant community structure among our site types using the basal area of stems greater than 2.5 cm DBH (see Supplementary Materials, Table S4 for complete model statistics). GLMs revealed that total basal area (native trees, exotic trees and tree ferns) was significantly higher at sites with tree ferns ($F_{1,12} = 8.1, p < 0.05$) but did not differ with variations in restoration status ($F_{1,12} = 0.002, p = 1.0$). The native tree basal area was significantly higher at restored sites ($F_{1,12} = 8.4, p < 0.05$) but did not vary significantly with tree fern presence ($F_{1,12} = 0.7, p = 0.7$). Furthermore, the tree fern basal area was significantly higher at sites with tree ferns ($F_{1,12} = 17.2, p < 0.01$), but restoration status had no significant effect ($F_{1,12} = 0.4, p = 0.5$). Finally, the exotic tree basal area did not vary significantly with the tree fern presence ($F_{1,12} = 3.8, p = 0.1$) or restoration status ($F_{1,12} = 1.0, p = 0.3$).

Figure 5 shows the basal areas for individual plant species across sites. Unrestored sites with tree ferns covered the highest average basal area ($25.7 \pm 12.2 \text{ m}^2 \text{ ha}^{-1}$), dominated by *Dicksonia squarrosa* (82%). Unrestored sites without tree ferns covered the lowest average basal area ($9.0 \pm 6.8 \text{ m}^2 \text{ ha}^{-1}$), with only a few exotic trees, such as *Salix cinerea* L. and *Alnus glutinosa* (L.) Gaertn. (Table S5, Supplementary Materials). Basal areas were more similar among restored sites, whether tree ferns were present ($18.5 \pm 3.3 \text{ m}^2 \text{ ha}^{-1}$) or absent ($18.4 \pm 3.4 \text{ m}^2 \text{ ha}^{-1}$). While unrestored sites with tree ferns were dominated by *D. squarrosa* (light yellow bars), restored sites with tree ferns achieved higher basal areas of *Cyathea dealbata* and *C. medullaris* (orange bars).

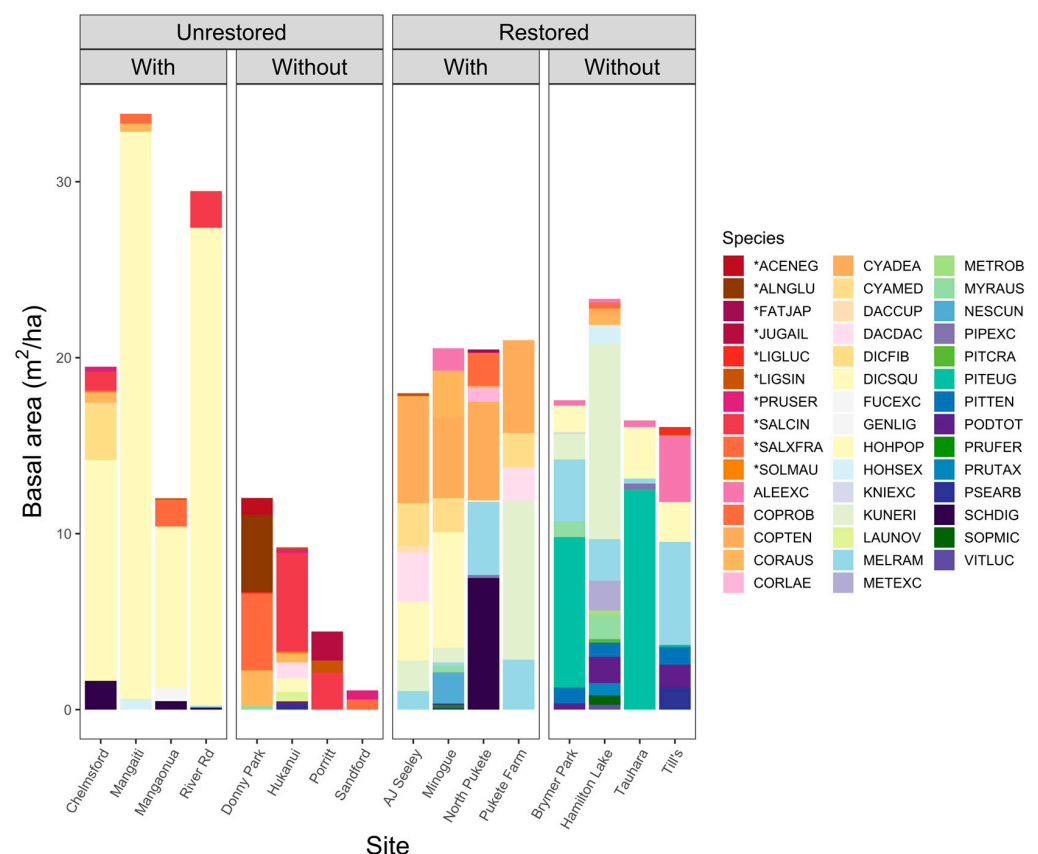


Figure 5. Tree and tree fern basal areas ($\text{m}^2 \text{ ha}^{-1}$) of vegetation plots measured in Hamilton, New Zealand. The 16 plots were assigned to our four site types based on restoration status (restored, unrestored) and the presence of tree ferns (with, without). An asterisk preceding the six-letter codes denotes an exotic species. Scientific and common names associated with the six-letter species codes are provided in Table A3.

3.4. Environmental Predictors of Plant Communities

We examined potential environmental predictors of individual plant groups and total native species richness across our site types. The GLM results identified environmental predictors correlated with plant community composition (Table 4). Rarefied native richness (Table 4) was positively influenced by the tree fern basal area ($z = 4.4$, $p < 0.001$) and the restoration age ($z = 4.4$, $p < 0.001$) but negatively influenced by the maximum tree height ($z = -3.0$, $p < 0.01$) and the average slope ($z = -1.6$, $p = 0.1$). Rarefied exotic species richness was negatively associated with tree fern basal area, but the relationship was not statistically significant at an alpha level of 0.05 ($z = -1.6$, $p = 0.1$, Table 4).

Table 4. Generalised linear model results investigating environmental predictors of native rarefied richness, exotic rarefied richness and rarefied richness per plant group (i.e., seedling, sapling, tree, ground fern and epiphyte richness). Environmental predictors were standardised (i.e., centred on the mean and scaled to unit variance). Incidence rate ratios with 95% confidence intervals (CIs) are provided. Statistically significant p -values at $\alpha = 0.05$ are in boldface.

Model	Predictors	Incidence Rate Ratio	95% CI	p -Value
Rarefied native richness (n = 200)	(Intercept)	14.46	12.58–16.49	<0.001
	Tree fern basal area	1.37	1.19–1.58	<0.001
	Restoration age	1.58	1.29–1.94	<0.001
	Maximum tree height	0.75	0.62–0.91	0.003
	Average slope	0.88	0.75–1.03	0.108
Rarefied exotic richness (n = 50)	(Intercept)	4.30	3.35–5.40	<0.001
	Tree fern basal area	0.82	0.63–1.05	0.117
Rarefied native seedling richness (n = 50)	(Intercept)	3.91	2.97–5.02	<0.001
	Restoration age	1.64	1.27–2.16	<0.001
Rarefied native sapling richness (n = 50)	(Intercept)	3.84	2.89–4.96	<0.001
	Restoration age	2.15	1.46–3.25	<0.001
	Tree fern basal area	1.20	0.91–1.58	0.194
	Maximum tree height	0.63	0.43–0.90	0.014
	Average slope	0.71	0.50–0.96	0.037
Rarefied native tree richness (n = 50)	(Intercept)	4.41	3.41–5.57	<0.001
	Restoration age	1.82	1.37–2.44	<0.001
	Maximum tree age	0.78	0.60–1.02	0.065
Rarefied ground fern richness (n = 50)	(Intercept)	2.59	1.81–3.53	<0.001
	Tree fern basal area	1.89	1.40–2.61	<0.001
Rarefied native epiphyte richness (n = 50)	(Intercept)	2.96	2.09–4.01	<0.001
	Tree fern basal area	2.35	1.77–3.20	<0.001

The environmental predictors influencing rarefied native species richness differed among individual plant groups. Table 4 shows that restoration age positively affected seedling ($z = 3.7$, $p < 0.001$) and tree species richness ($z = 4.1$, $p < 0.001$). Native sapling species richness (Table 4) was also positively influenced by restoration age ($z = 3.8$, $p < 0.001$) but was negatively influenced by maximum height ($z = -2.5$, $p < 0.05$) and average slope ($z = -2.1$, $p < 0.05$). Although not statistically significant at an alpha level of 0.05, tree fern basal area positively affected rarefied native sapling richness (Table 4). Table 4 also shows strong positive relationships between the tree fern basal area and rarefied ground fern ($z = 4.0$, $p < 0.001$) and epiphyte richness ($z = 5.7$, $p < 0.001$).

Our distance-based redundancy analysis (dbRDA) found significant correlations between tree fern basal area and restoration age, with differences in plant community composition by abundances across sites (Figure A2). Variation partitioning revealed the amount of variation ($R^2 = 0.29$) in plant community composition explained by tree fern basal area and restoration age, with slightly more variation explained independently by the tree fern basal area ($F_{1,13} = 3.2$, $p < 0.01$, $R^2 = 0.15$) than the restoration age ($F_{1,13} = 3.3$, $p < 0.01$, $R^2 = 0.14$). There was no shared variation explained by these two environmental variables.

4. Discussion

We identified distinct plant communities associated with restoration status and tree fern presence. Higher native plant richness at restored sites without tree ferns was partially driven by increased plant abundances, with more diverse woody pioneer communities. In contrast, the presence of tree ferns at unrestored sites supported higher native species richness with more diverse epiphyte and ground fern assemblages. Most epiphytes (approximately 90%) were on tree ferns, and 65% of ground ferns only occurred in plots with tree ferns. Tree ferns provide a thick root mantle and fibrous substrate with high moisture retention that is conducive to epiphyte establishment [58]. Hence, tree ferns appear to augment native species richness by providing a suitable habitat for these plant groups. These results highlight the strong association between tree ferns, epiphytes and ground ferns, three functionally diverse plant groups that contribute to ecosystem processes [59,60]. Additionally, increased basal areas (i.e., an indicator of biomass) at our sites with tree ferns showed the significant effect that tree ferns can have on plant community structure and composition. Our results, therefore, show that the presence of tree ferns can enhance native species richness and the functioning of urban ecosystems via richer epiphyte and ground fern assemblages.

4.1. Community Assembly and Succession

We found a range of differences in plant composition among our site types, suggesting that early-arriving tree ferns significantly impact plant community composition and assembly [23]. The most abundant tree fern at unrestored sites was *Dicksonia squarrosa*, while *Cyathea medullaris* and *C. dealbata* were more abundant at restored sites. Restored sites with tree ferns also had fewer native seedlings, saplings and trees (i.e., angiosperms and conifers), signalling competitive relationships among these groups, which is consistent with previous research [61]. Where priority effects lead to tree ferns establishing first, a positive feedback loop may prevent other species from establishing and occasionally inhibit successional processes [14,62,63]. Our results suggest that tree ferns do not inhibit some shade-tolerant species and, with the natural or assisted arrival of these species, may assist the successional pathway towards broadleaved-conifer forest.

In urban restoration, enrichment planting (i.e., planting late-successional species in the understory of pioneer communities) is critical for replacing short-lived pioneers with long-lived species [35]. Little to no enrichment planting has been undertaken at our restored sites, and few late successional species were recorded in any of our site types. Species such as *Dacrydium cupressinum*, *Alectryon excelsus* Gaertn. and *Hedycarya arborea* J.R.Forst. & G.Forst. have been sparsely planted at some restored sites.

We did not directly investigate successional pathways using remeasurement of tree fern communities over time; however, community composition on our chronosequence may signal potential pathways. Tree ferns are primarily considered mid-late successional species, although species including *Dicksonia squarrosa* and *Cyathea medullaris* can dominate early successional stages. Higher native sapling species richness at our unrestored sites with tree ferns suggests that tree ferns may assist species regeneration. Furthermore, our

sites with tree ferns supported some shade-tolerant broadleaf species (e.g., *Schefflera digitata* J.R.Forst. & G.Forst.), which aligns with a previous study where tree ferns did not inhibit shade-tolerant species [28]. Putative pathways following these communities include the development of a broadleaf understory after 40 years and conifer-broadleaf forest after 80–100 years [12,30,64].

4.2. Study Limitations

Whilst our results suggest that tree ferns can act as ecological filters, thereby altering plant community composition, our study faced some limitations. First, our statistical power was limited by the sites available that met the criteria for site selection (i.e., $n = 4$ per site type; Table S1), which could have reduced our ability to statistically identify differences (i.e., increased chance of Type II errors); however, in many cases, our analyses detected significant ($\alpha = 0.05$) differences among the treatments. Second, species richness is expected to increase with time. Although we controlled for plot restoration age (i.e., the time since native planting began) in our statistical analyses as a covariate, the age of sites dominated by tree ferns was difficult to verify because, unlike the woody species we dated, they do not exhibit annual growth rings. Third, our study design was a mensurative experiment, and sites with tree ferns may be confounded by other variables. While our results signal the importance of retaining extant tree ferns, experimentally planting them at restoration sites and observing long-term successional trajectories would provide additional insights into their role in shaping community composition.

4.3. Implications for Urban Ecological Restoration

Standard restoration practice focuses on restoring pioneer trees and shrubs, such as *Leptospermum scoparium* and *Kunzea ericoides*, without recognising the ecological value of pioneer tree ferns. Pioneer trees are favoured because they are easily sourced and affordable. In contrast, ferns are rarely available from restoration nurseries. Pioneer trees also grow faster than tree ferns. In two decades, *Kunzea ericoides* can reach 7 m in height [29], compared to *Cyathea medullaris* (2.3 m) and *Dicksonia squarrosa* (1 m) [65].

Our results highlight the need to protect extant tree ferns, as they can augment native species richness and enhance opportunities for urban restoration projects. Although monospecific colonies can arrest succession [14], we found tree fern communities to support higher native species richness, providing a habitat for ground ferns and epiphytes, which are both poorly represented functional groups in urban forests [66,67]. Extant tree fern stands also provide the advantage of a native-dominated canopy from the outset of restoration projects. Establishing and maintaining a canopy is critical to the success of ecological restoration projects [68]. A developed canopy slows the establishment and growth of light-demanding invasive plants that compete with native species [69]. However, a canopy can take several decades to reinstate, requiring ongoing labour to release native trees from exotic species that persist in high light levels. Our sites with tree ferns were associated with reduced exotic species abundance. Therefore, using extant tree ferns, rather than replacing them with pioneer trees, could advance restoration progress.

A bespoke approach, planting pioneers best suited to the site conditions, should be employed in urban restoration. Determining which pioneer species are appropriate for a site should be guided by their ecology (e.g., growth strategy and habitat). *Kunzea ericoides* and *Leptospermum scoparium* generally colonise drier sites [28], and tree ferns occur on hillslopes and gullies or depressions. Dense stoloniferous thickets of *Dicksonia squarrosa* may restrict tree regeneration but support diverse epiphyte communities. These stands may require manipulation (i.e., reducing the cover or density of dominant canopy species to increase diversity) to prevent monospecific, self-perpetuating thickets and allow tree regeneration

or enrichment planting without diminishing epiphyte diversity. In contrast, monopodial *Cyathea medullaris* and *C. dealbata* may require less thinning. Studies manipulating tree fern stands have primarily included binary treatment groups [16] or frond thinning trials [61], but there is a lack of long-term research measuring community composition along a gradient of tree fern densities.

We identified some potential environmental predictors of our distinct plant communities, including restoration age and tree fern basal area. Slope and the maximum canopy height also negatively affected native species richness, possibly due to reduced soil moisture on steeper sites and inadequate enrichment planting beneath tall pioneer trees. Furthermore, tree fern basal areas positively influenced native epiphyte and ground fern species richness and negatively affected exotic species richness.

5. Conclusions

In conclusion, our results highlight the ecological value of extant tree ferns in augmenting native species richness, supporting functional groups like ground ferns and epiphytes and potentially suppressing exotic species by providing an early canopy. Incorporating pioneer tree ferns into restoration practice will encourage the diversification of plant communities and the range of species and life forms they support. Tree fern basal area and restoration age significantly contributed to our distinct plant communities, but further research on epiphyte functional traits and environmental drivers is necessary to better understand epiphyte–host and epiphyte–environment relationships. Long-term quantitative research on how tree fern density influences community composition is also needed to determine thresholds for maximising indigenous plant diversity in urban ecosystems. Overall, our study suggests a need to reconsider current restoration practices that often overlook or remove tree ferns in favour of faster-growing pioneer trees.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/f16091498/s1>, Table S1: Site age and history of the sixteen vegetation plots; Figure S1: Vegetation plot design (200 m²); Figure S2: Variation partitioning of the effects of tree fern basal area and restoration age on community composition; Table S2: Generalised linear model results testing the effect of tree fern presence and restoration status on total native abundances, rarefied species richness, exotic plant abundances and rarefied richness; Table S3: Pairwise comparisons of native vascular plant communities among the four site types; Table S4: Generalised linear model results testing the effect of tree fern presence and restoration status on total basal area (exotic trees, native trees and tree ferns), native woody tree basal area, tree fern basal areas and exotic tree basal area; Table S5: Three leading dominant trees or tree ferns for each site type.

Author Contributions: Conceptualisation, H.C.R. and B.D.C.; methodology, H.C.R.; software, H.C.R.; validation, H.C.R., F.J.B. and B.D.C.; formal analysis, H.C.R. and F.J.B.; investigation, H.C.R.; resources, B.D.C.; data curation, H.C.R.; writing—original draft preparation, H.C.R.; writing—review and editing, H.C.R., F.J.B. and B.D.C.; visualisation, H.C.R.; supervision, F.J.B. and B.D.C.; project administration, H.C.R.; funding acquisition, B.D.C. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The datasets generated and analysed during the study are available from the corresponding author upon reasonable request.

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

Abbreviations

The following abbreviations are used in this manuscript:

DBH	Diameter at breast height
dbRDA	Distance-based redundancy analysis
GLM	Generalised linear model
HCC	Hamilton City Council
NMDS	Nonmetric multidimensional scaling
PCaN	People, Cities & Nature Programme
PERMANOVA	Permutational multivariate analysis of variance

Appendix A

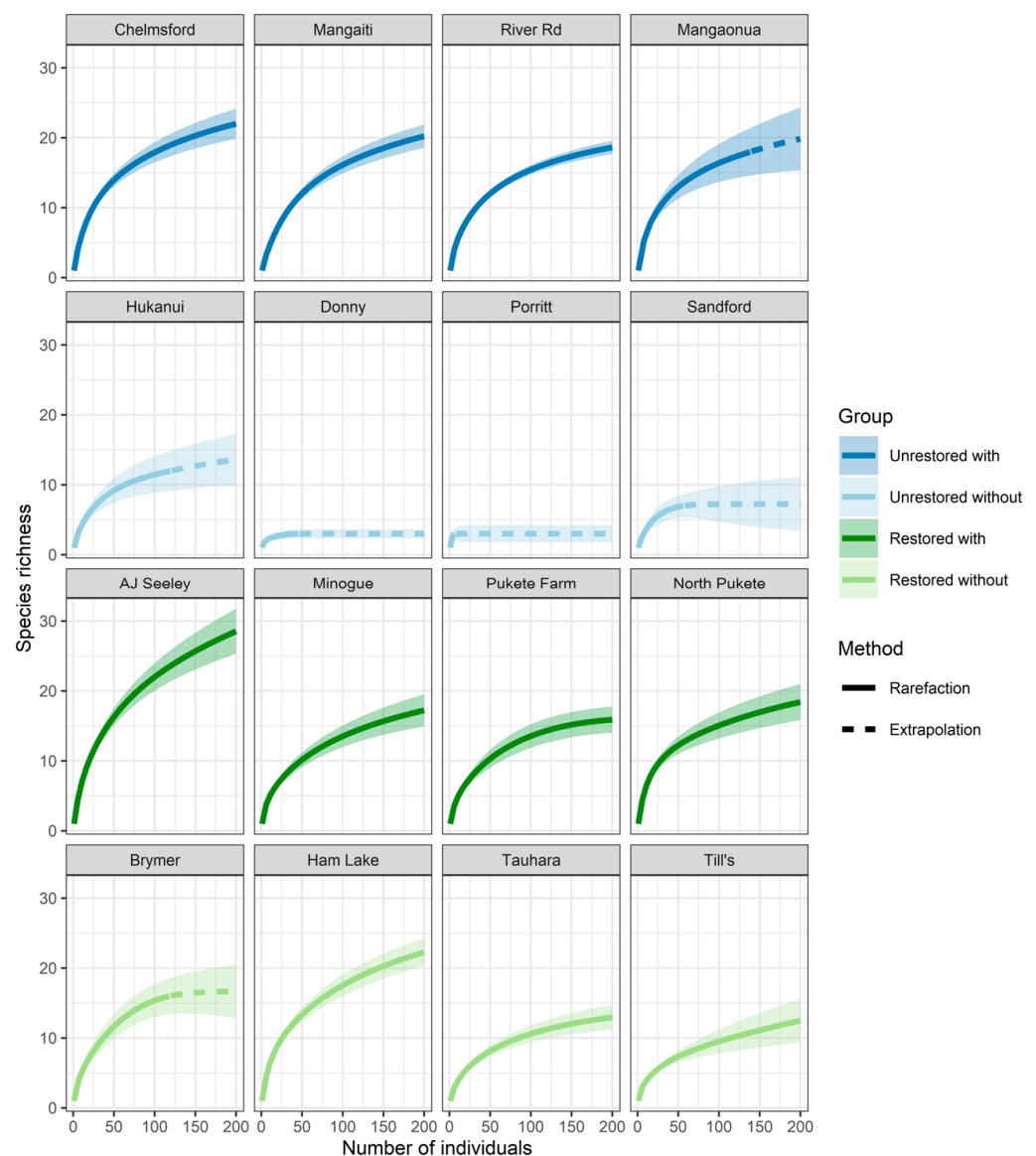


Figure A1. Rarefaction and extrapolation curves for each plot. Data were extrapolated to 200 individuals to investigate whether sampling intensity satisfied the expected native species richness. Colours represent the four study groups: unrestored with tree ferns (dark blue), unrestored without (light blue), restored with (dark green) and restored without (light green).

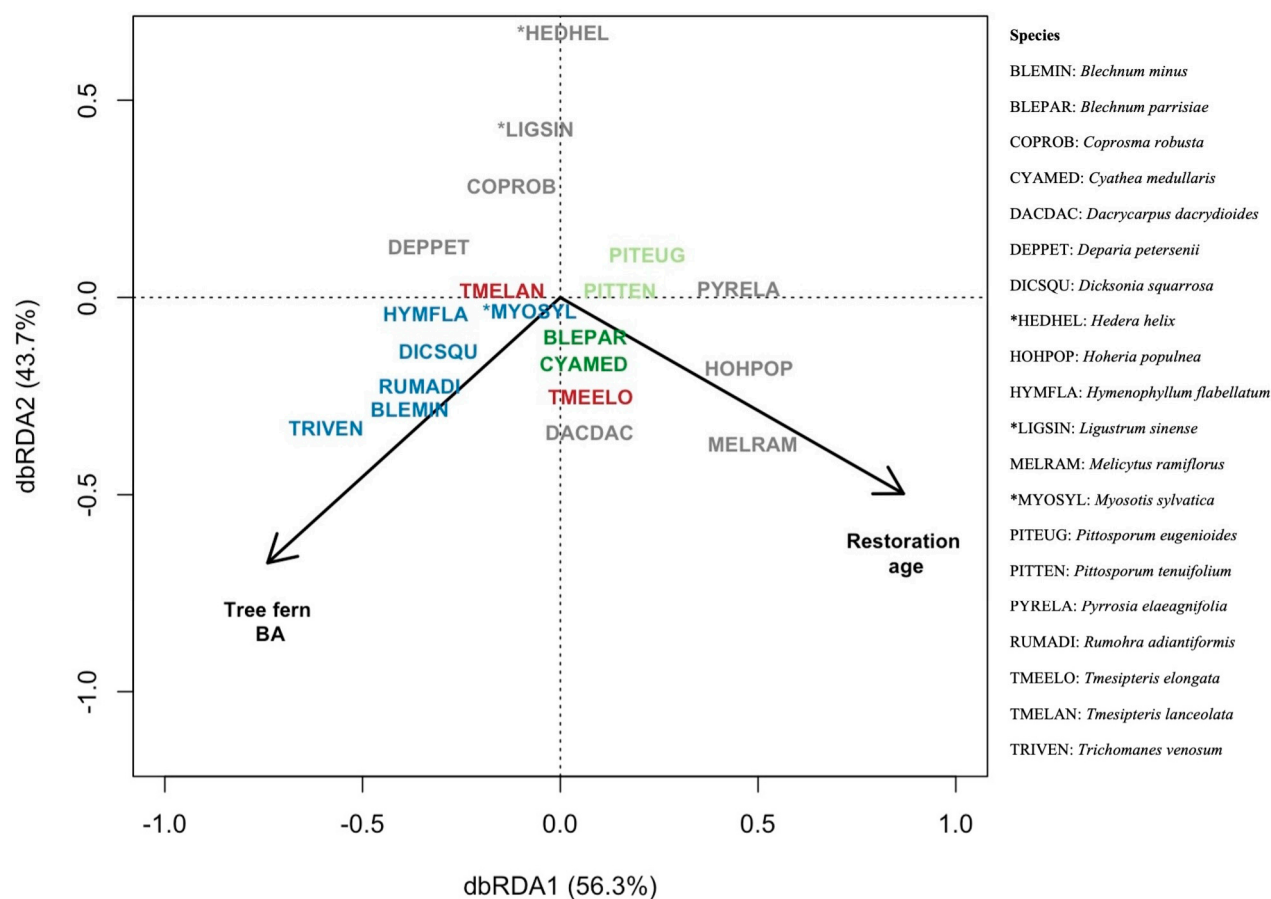


Figure A2. Redundancy analysis (RDA) of the effect of restoration age and tree fern basal area (BA) on influential species (six-letter codes). Our study groups were based on restoration status (restored, unrestored) and the presence of tree ferns (with, without). Species colours represent indicator species of the study groups: restored sites with tree ferns (dark green), restored sites without tree ferns (light green) and unrestored sites with tree ferns (dark blue). Species in grey are eight of the most abundant species, and red species (2) represent indicator species of unrestored sites with tree ferns that are also abundant species. These ten most abundant species accounted for 62% of the mean relative abundance. An asterisk denotes an exotic species.

Appendix B

Table A1. Pairwise comparisons of vascular plant communities (native and exotic abundances) among the four site types using a permutational multivariate analysis of variance (PERMANOVA) and accounting for restoration age (i.e., years since native plantings started) as a covariate.

Group 1	Group 2	F-Value	R ²	p-Value
Unrestored without	Restored with	2.23	0.47	<0.05
Unrestored without	Restored without	2.25	0.47	<0.05
Unrestored with	Restored with	2.58	0.51	<0.05
Unrestored with	Unrestored without	4.61	0.43	<0.05
Unrestored with	Restored without	4.68	0.65	<0.05
Restored with	Restored without	0.87	0.13	0.68

Table A2. Indicator species associated with three of our site types. Indicator values represent the strength of the relationship between the species abundances and the site type; values closer to 1 signal stronger associations. An asterisk denotes an exotic species.

Site Type	Species	Indicator Value	p-Value
Unrestored sites with tree ferns	<i>Tmesipteris elongata</i>	1.00	<0.01
	<i>Tmesipteris lanceolata</i>	0.92	<0.01
	<i>Trichomanes venosum</i>	0.96	<0.01
	<i>Blechnum minus</i>	0.93	<0.01
	<i>Rumohra adiantiformis</i>	0.87	<0.05
	<i>Dicksonia squarrosa</i>	0.89	<0.01
	<i>Hymenophyllum flabellatum</i>	0.87	<0.05
	* <i>Myosotis sylvatica</i>	0.87	<0.05
Restored sites with tree ferns	<i>Blechnum parrisiae</i>	0.87	<0.05
	<i>Cyathea medullaris</i>	0.87	<0.05
Restored sites without tree ferns	<i>Pittosporum eugeniioides</i>	0.97	<0.01
	<i>Pittosporum tenuifolium</i>	0.80	<0.05

Table A3. Scientific names associated with the six-letter species codes presented in the trees and tree fern basal area facet plot (see Figure 5). Common and family names are also provided.

Status	Six-Letter Code	Scientific Name	Common Name	Family
Exotic	ACNEG	<i>Acer negundo</i>	Box elder	Sapindaceae
	ALNGLU	<i>Alnus glutinosa</i>	Alder	Betulaceae
	FATJAP	<i>Fatsia japonica</i>	Fatsia	Araliaceae
	JUGAIL	<i>Juglans ailantifolia</i>	Japanese walnut	Juglandaceae
	LIGLUC	<i>Ligustrum lucidum</i>	Tree privet	Oleaceae
	LIGSIN	<i>Ligustrum sinense</i>	Chinese privet	Oleaceae
	PRUSER	<i>Prunus serrulata</i>	Japanese cherry	Rosaceae
	SALCIN	<i>Salix cinerea</i>	Grey willow	Salicaceae
	SALXFRA	<i>Salix ×fragilis</i>	Crack willow	Salicaceae
	SOLMAU	<i>Solanum mauritianum</i>	Woolly nightshade	Solanaceae
Native	ALEEXC	<i>Alectryon excelsus</i>	Titoki	Sapindaceae
	COPROB	<i>Coprosma robusta</i>	Karamū	Rubiaceae
	COPTEN	<i>Coprosma tenuicaulis</i>	Hukihuki	Rubiaceae
	CORAUS	<i>Cordyline australis</i>	Ti kōuka	Asparagaceae
	CORLAE	<i>Corynocarpus laevigatus</i>	Karaka	Corynocarpaceae
	CYADEA	<i>Cyathea dealbata</i>	Ponga	Cyatheaceae
	CYAMED	<i>Cyathea medullaris</i>	Mamaku	Cyatheaceae
	DACCUP	<i>Dacrydium cupressinum</i>	Rimu	Podocarpaceae
	DACDAC	<i>Dacrycarpus dacrydioides</i>	Kahikatea	Podocarpaceae
	DICFIB	<i>Dicksonia fibrosa</i>	Whekī-ponga	Dicksoniaceae
	DICSQU	<i>Dicksonia squarrosa</i>	Whekī	Dicksoniaceae
	FUCEXC	<i>Fuchsia excorticata</i>	Kōtukutuku	Onagraceae
	GENLIG	<i>Geniostoma ligustrifolium</i>	Hangehange	Loganiaceae
	HOHPOP	<i>Hoheria populnea</i>	Houhere	Malvaceae
	HOHSEX	<i>Hoheria sextylosa</i>	Houhere	Malvaceae
	KNIEXC	<i>Knightia excelsa</i>	Rewarewa	Proteaceae
	KUNERI	<i>Kunzea ericoides</i>	Kānuka	Myrtaceae
	LAUNOV	<i>Laurelia novae-zelandiae</i>	Pukatea	Atherospermataceae
	MELRAM	<i>Melicytus ramiflorus</i>	Māhoe	Violaceae
	METEXC	<i>Metrosideros excelsa</i>	Pōhutukawa	Myrtaceae

Table A3. Cont.

Status	Six-Letter Code	Scientific Name	Common Name	Family
	METROB	<i>Metrosideros robusta</i>	Northern rātā	Myrtaceae
	MYRAUS	<i>Myrsine australis</i>	Red mapou	Primulaceae
	NESCUN	<i>Nestegis cunninghamii</i>	Black maire	Oleaceae
	PIPEXC	<i>Piper excelsum</i>	Kawakawa	Piperaceae
	PITCRA	<i>Pittosporum crassifolium</i>	Karo	Pittosporaceae
	PITEUG	<i>Pittosporum eugenoides</i>	Tarata	Pittosporaceae
	PITTEN	<i>Pittosporum tenuifolium</i>	Kōhūhū	Pittosporaceae
	PODTOT	<i>Podocarpus totara</i>	Tōtara	Podocarpaceae
	PRUFER	<i>Prumnopitys ferruginea</i>	Miro	Podocarpaceae
	PRUTAX	<i>Prumnopitys taxifolia</i>	Mataī	Podocarpaceae
	PSEARB	<i>Pseudopanax arboreus</i>	Whauwhaupaku	Araliaceae
	SCHDIG	<i>Schefflera digitata</i>	Patē	Araliaceae
	SOPMIC	<i>Sophora microphylla</i>	Kōwhai	Fabaceae
	VITLUC	<i>Vitex lucens</i>	Pūriri	Lamiaceae

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