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A comparative analysis of three remnant tōtara dune forest patches in the peri-urban fringe of Waihōpai / Invercargill, Murihiku / Southland, Aotearoa / New Zealand

Yannick Dorsman[1]*, Jordon Traill[1]*

Affiliations:

1. **Southern Institute of Technology, 133 Tay Street, Invercargill, New Zealand**

* **Corresponding author: yannickd@tutanota.com**

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Abstract

The tōtara (*Podocarpus totara* G.Benn. ex D.Don var. *totara*) dune forests on the fringe of Waihōpai / Invercargill are one of the largest remaining tracts of this threatened forest association. Their proximity to an urban centre exposes the forest to threats, but there is also the potential for restoration through community participation. Effective restoration requires informed knowledge of the ecological characteristics of nearby sites of reference. This study compares vascular plant communities across three sites: two intact tōtara dune forest sites managed by Invercargill City Council, and a site under a restoration management regime where stock grazing was recently ended. Four plots at each site were surveyed to compare plant assemblages to infer successional pathways and patch resilience. The two reference sites, while having similar elevation, slope, aspect and canopy species, held differences in mid-canopy woody species, indicating that dune age and forest condition could drive below-canopy species assemblages. Six species were identified as widespread within the intact patches but absent in the degraded site, suggesting potential target restoration plantings for tōtara dune forests in the region.

Keywords

Podocarpus totara var. *totara*, *Podocarpus laetus*, coastal tōtara dune forest, Sandy Point Domain, Fosbender Park, Ōreti Tōtara Dune Forest, Aotearoa / New Zealand, restoration

Introduction

Stable sand-dune forest ecosystems are endangered in Aotearoa / New Zealand due to a history of conversion to farmlands and plantations (Holdaway et al. 2012). The Sandy Point and Ōtātara peninsulas on the peri-urban fringe of Waihōpai / Invercargill hold some of the largest remaining tracts of tōtara (*Podocarpus totara* G.Benn. ex D.Don var. *totara*) dune forest, making the area of national significance in Aotearoa / New Zealand for this forest association (Southland Regional Council 2017; Singers & Rogers 2014; Harding 1999; Norton 2000). The landscape has retained a moderately high level of ecological integrity, with large remnant blocks protected on a mixture of private and public land.

While the tōtara dune forest's proximity to an urban area can contribute to ecological stress, it is also a potential source of restoration. Remnant forests near urban areas can suffer from exposure to anthropogenic stressors such as naturalised species invasion (LaPaix et al. 2012), rubbish dumping (Stenhouse 2004) and human disturbance (Bagnall 1979); however, this proximity can present cost-effective opportunities for restoration and maintenance of biodiversity values (Perni et al. 2021).

The remnant tōtara dune forest ecosystem lies in disjunct patches across the Sandy Point and Ōtātara peninsulas (Figure 1). At Sandy Point, three large disjunct fragments occur within the Sandy Point Domain and are managed by Invercargill City Council. The fragments on the Ōtātara Peninsula cover a larger area and are primarily located on private land within semiurban and farmland lifestyle blocks.

The fragmented distribution of the dune forests is both natural and anthropogenic. Natural drivers of distribution include barriers created by wetlands, rivers and sand inundation from advancing dunes. Since the mid-19th century, change has been accelerated through direct clearing for timber milling and agriculture, forestry and recent development of residential plots (Invercargill City Council 2013). These land-use changes have increased the fragmented characteristic of the forest, which can have negative impacts on remaining forest patches through increased exposure to edge effects (Forman & Godron 1986; Reed et al. 1996; McGarigal & Cushman 2002), altered forest structure (Echeverría et al. 2007), increased prevalence of invasive species (Ross et al. 2002) and reduced dispersal potential (Moran et al. 2009). As forests become increasingly fragmented, the ability for ecological regenerative processes can be diminished (Botzat et al 2015; Stenhouse 2004).

For decades, the Waihōpai / Invercargill community and council have led active restoration and conservation management programmes for this forest association. In Ōtātara, the Native Forest Restoration Trust (NFRT) purchased a 73-hectare property in 2020, of which 40 ha was previously grazed forest, that the Trust is now restoring (Native Forest Restoration Trust 2021). To better protect and restore the degraded remnant patches of this forest association, the stakeholders responsible for the restoration and conservation of the area need a full understanding of the suite of species that occurs within tōtara dune forest fragments in the context of the wider landscape. Restoration planning for degraded sites can be enhanced through access to detailed ecological knowledge of nearby reference sites.

A key requirement for the management and restoration of tōtara dune forest fragments is understanding of the successional pathways following disturbance. Knowledge of the diverse understorey and subcanopy of woody species present can reveal the regenerative potential of the forest (Wotton & McAlpine 2013). In instances where there is limited biomass or scant understorey woody species, the successional pathways of the area become harder to predict and could indicate a modified ecological process. The successional pathways for tōtara dune forests in the Murihiku / Southland context are not well documented or researched.

This study aims to document successional pathways along a gradient of fragmentation and degradation through an ecological comparison of three remnant sites: two intact and one under restoration management. This comparison will identify critical species and ecological processes, both present or absent, to develop understanding of coastal tōtara dune forest systems and inform restoration management.

Methods

The three sites measured were the Ōreti Road fragment (-46.450087, 168.271923), under active restoration management by NFRT, and two intact sites currently managed by the Invercargill City Council and located approximately equidistant to the north and south of the city (Figure 1). The southern patch, Daffodil Bay (-46.472328, 168.28939), is the largest and most intact remnant, and the northern patch, Fosbender (-46.427204, 168.259606), was chosen for its intermediate state of fragmentation and comparative

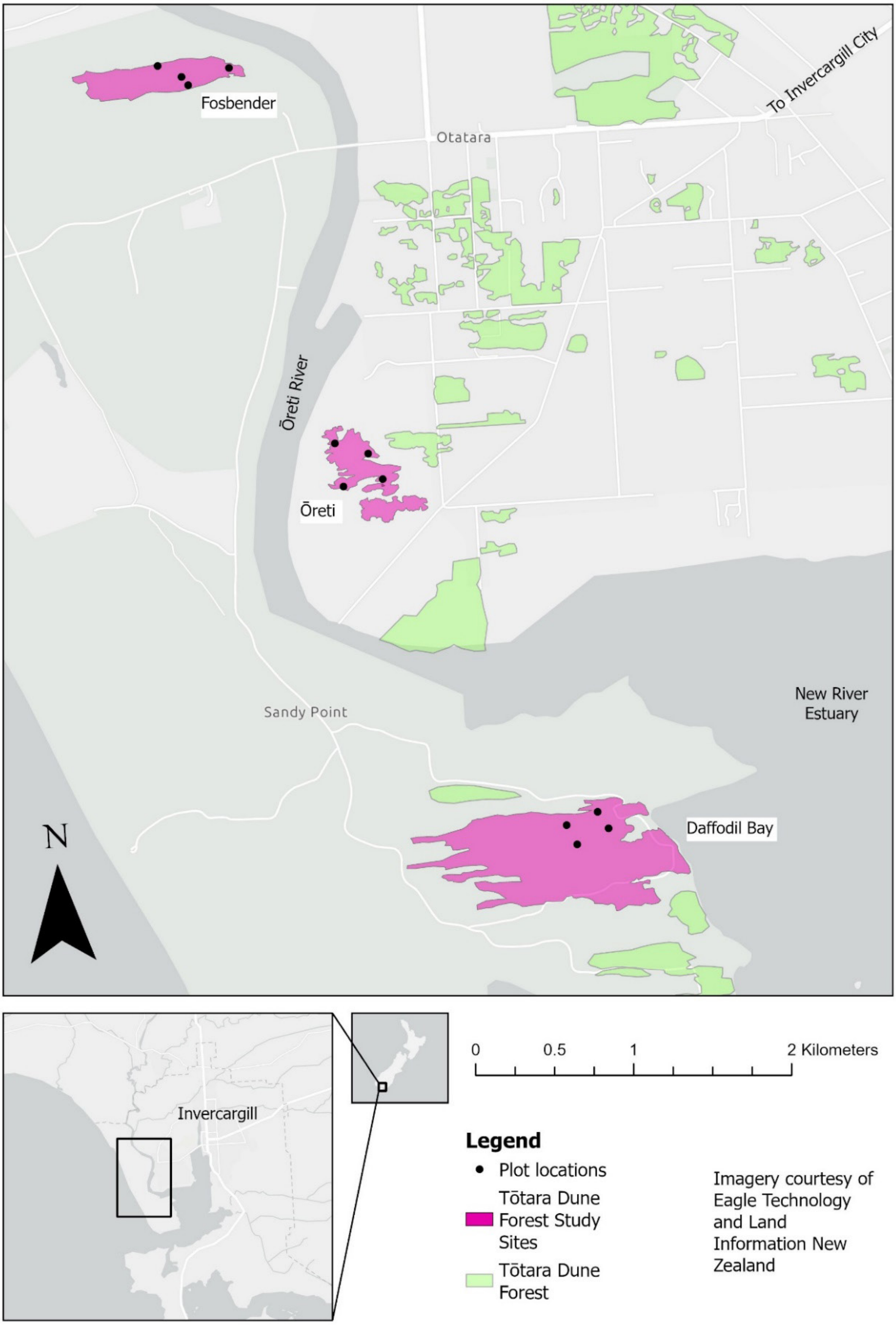

Figure 1. Plot locations within the Sandy Point–Ōtātara landscape with tōtara dune forest fragments coloured, study sites highlighted in purple and other remnant tōtara dune forests highlighted in green.

isolation. Rapid biodiversity assessments of the areas adjacent to each patch were carried out by the research team to understand surrounding habitat types. Using ArcGIS software, the landscape matrix of the tōtara dune forest remnants was mapped, as well as the size, shape and comparative isolation of the study sites. This information was gathered using ground-truthing techniques, previous surveys conducted by the researchers, and local knowledge.

Four surveys were conducted in each of the three sites to identify plot locations. As species composition within forests is influenced by aspect, slope and altitude (Bale et al. 1998), plot locations were selected based on aspect and slope equivalency with existing permanent plots. The Hurst and Allen Permanent Plot Method was adapted and modified for this research so direct comparison could be made with existing permanent plots in the area and against reports from the Department of Conservation's national Biodiversity Inventory and Monitoring programme.

Data was supplied by the NFRT from two permanent plots they surveyed in October 2021, in which one of the authors participated, and the methods used to collect the data followed the Hurst and Allen Permanent Plot Method. In autumn and spring 2022 the survey team located four sites within the intact remnants with similar aspect and slope, and a further two sites within the restoration management area. In total, 12 plots were measured once – ten plots by the survey team over an 18-month period, and two by a team from NFRT the previous year. All plots were collected following the Hurst and Allen Permanent Plot Method, and all data was collected over spring or autumn months.

After identifying a location that met the equivalency requirements, a random number generator was used to determine a bearing and step count leading to the corner of the plot. From here the plot was laid out. The back-Recce sapling and understorey plot methods were used as outlined in Hurst and Allen (2007) to provide insights into the species richness, diversity, composition and structure of the tōtara dune forests, and to identify key species guilds and associations.

A full-Recce method measure was conducted at each plot, with height and cover classes recorded of all species present. The data collected within the Recce measure quantified plot-species richness and forest structure at each plot. Additional surveys including sapling counts and seedling sub-plots were conducted to supplement this data. A subset of the total potential subplots measured was formed, and this arrangement was repeated through every plot. Fifty percent of the plot was sampled using the sapling-count method, and five of the 24 seedling subplots were measured following the Hurst and Allen method.

The seedling-subplot method is largely used to measure changes in seedling-height classes and regeneration through time (McNutt 2012). This interrogation lay largely outside of the scope of this research, as species richness, heights and cover classes were collected through the back-Recce method within the Hurst and Allen plot design. For sapling subplots, a random number generator was used to obtain eight numbers from one to 16, these corresponding to a letter's position in the alphabet. The data provided by NFRT was spliced to select the same plot configuration.

To counter the greater diversity with increased patch size, a section of the Daffodil Bay site was surveyed. As the Daffodil Bay site was significantly larger than the other two, a targeted approach covering an area comparable with the other two fragments was chosen. Rather than aiming to identify turnover through space, this was carried out to better understand species composition in the Daffodil Bay site as a reference for the Ōreti Road site.

From the collected data, comparisons within and between sites were made regarding species composition and forest structure. The analysis was focused on identifying species absence and presence in different strata, alongside prevalence of indigenous species and woody weeds to understand key differences, and to identify critical species that may be present or absent within the restoration and remnant sites.

Results

Site characteristics

All sites are coastal – the ocean is approximately 2.5 km from each site – with close proximity to New River Estuary and the Ōreti River mouth. All sites feature undulating topography ranging from sea level to 35 metres. Daffodil Bay and Fosbender consist of a patchwork of stable dune deposits, ranging in age from 14,000 years old to new; and the Ōreti Road site consists of Late Pleistocene river deposits with Holocene windblown deposits on top ranging from 14,000 to 70,000 years old (GNS Science Te Pū Ao 2014).

The Daffodil Bay tōtara forest fragment (72.7 ha, perimeter 8.2 km) is largely rectangular with fingers

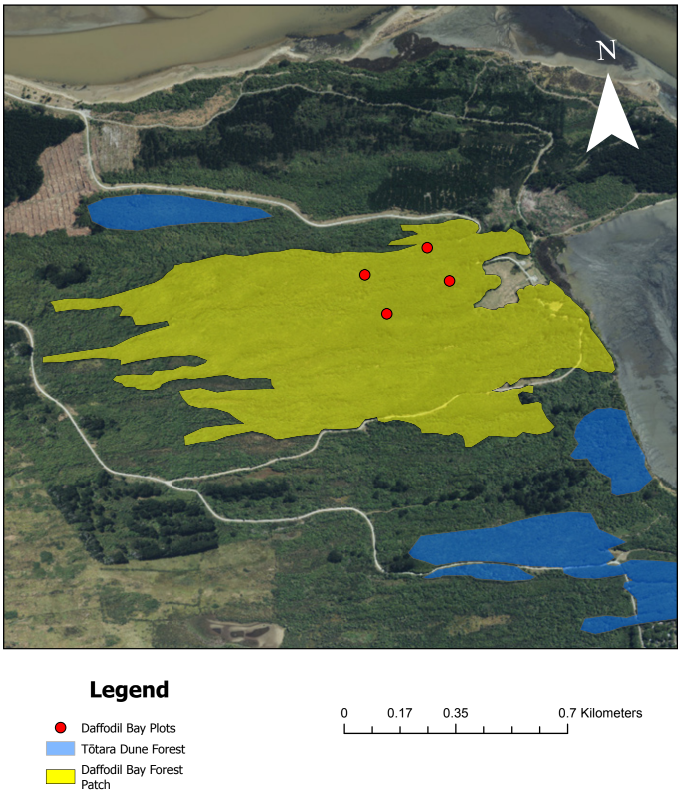

Figure 2. Daffodil Bay tōtara dune forest with plot locations. Forest is surrounded by *Pittosporum tenuifolium*- and *P. eugenioides*-dominated regenerating forest.

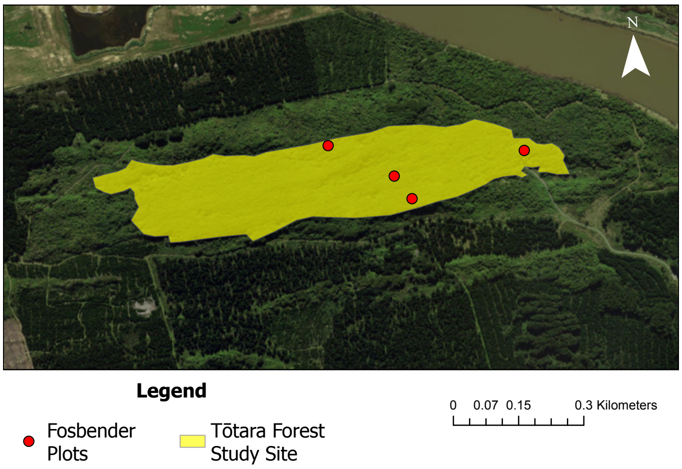

Figure 3. The Fosbender tōtara dune forest with plot locations.

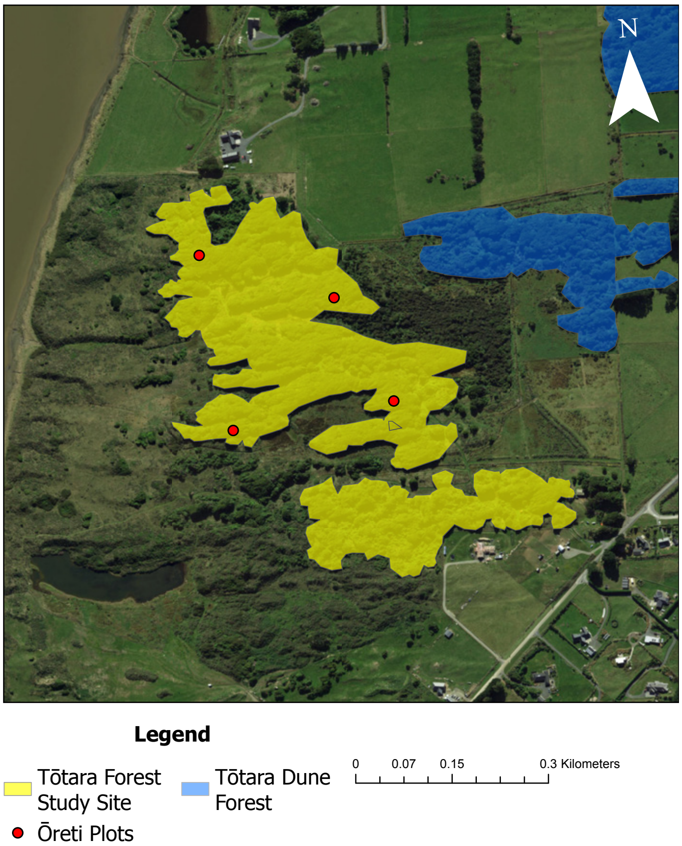

Figure 4. The Ōreti Tōtara Dune Forest patch with plot locations.

of tōtara forest extending along ridgelines to the west (Figure 2). The area contains some damp hollows of mānuka–*Coprosma* shrubland in the interior. Two other tōtara dune forest fragments that were outside the study site occur to the north and south, 75 m and 320 m away respectively. Importantly, these patches are connected and buffered by a large area of mixed broadleaf forest with a canopy dominated by *Pittosporum tenuifolium* Gaertn. and *P. eugenioides* A.Cunn with a combined area (inclusive of all tōtara dune forests) of 365 ha. Within this buffering forest are stands of macrocarpa (*Hesperocyparis macrocarpa* (Hartw.) Bartel).

The Fosbender tōtara forest fragment (16.6 ha, perimeter 2.5 km) has a narrow rectangular shape (Figure 3) and is the most isolated from the closest tōtara dune forest fragment (1.15 km). A stand of tōtara is present 50 m northwest (approximately 0.55 ha), and to the northeast there is a small fragment (approximately 3.45 ha) of mixed broadleaf and tōtara. The Fosbender patch is an entirely closed-canopy tōtara–mataī forest skirted by a thin area of mixed broadleaf scrub forest comprising *P. tenuifolium*, *Aristotelia serrata* (J.R.Forst. et G.Forst.) W.R.B.Oliv. and *Coprosma propinqua* A.Cunn. var. *propinqua* (hereafter referred to as *C. propinqua*). The areas surrounding the tōtara forest are largely smothered by *Muehlenbeckia australis* (G.Forst.) Meisn. vineland. Toward the north and south, there is an abrupt ecocline into *Pinus radiata* D.Don plantation forestry with an understorey consisting primarily of non-indigenous species such as *Rubus fruticosus* complex and various pasture species.

The Ōreti Road fragment is the smallest study site (14.9 ha, perimeter 4.8 km) and has an interrupted canopy with large areas of former farm tracks and grassy clearings (Figure 4). The site has smaller satellite patches of tōtara forest 130 and 50 m away, and is bordered by pasture to the north, west and south with isolated trees (indigenous and non-indigenous) and shrubs. On the eastern boundary of the forest lies a mānuka (*Leptospermum scoparium* J.R.Forst. et G.Forst.) and *Coprosma* spp.-dominated wetland area.

Vascular flora and species richness

Within the combined study area, 80 species of vascular plants were identified: 57 indigenous and 23 non-indigenous (Appendix 1). Among the indigenous species, no threatened plant taxa were identified as per de Lange et al. (2024). The Ōreti Road site showed the largest number of total species and number of indigenous vascular plant species (Table 1). However, indigenous dominance increased along a gradient of forest patch size: the Daffodil Bay site with 100% dominance, the Fosbender site with 91%, and the Ōreti Road site with 61% dominance. Understorey vegetation cover and sapling density were substantially higher in both reference sites in comparison to the Ōreti Road site.

At the Fosbender site, 14 indigenous woody species and two non-indigenous woody species were identified. Daffodil Bay had 31 species in total, all indigenous, with 19 woody species. This was the largest patch, and had the highest indigenous dominance and number of indigenous woody species. Indigenous non-woody species richness was highest at the Ōreti Road site, with 46 species, and lower at the Fosbender (10) and Daffodil Bay (12) sites.

Comparison of forest structure

At all plots across the three sites, the canopy was dominated by two species of tōtara, *Podocarpus totara* and *P. laetus*. Hooibr. ex Endl. Hybrids of the two were also common throughout, along with scattered individuals of mataī (*Prumnopitys taxifolia* (Sol. ex D.Don) de Laub.). Canopies in all sites were considered closed, that is, with continuous cover greater than 70%, and had an average canopy height of 5 to 20 m, determined by where the plot was located on the dune and the height of the dune itself. Daffodil Bay was the only site where angiosperms were recorded at canopy level. *Pittosporum eugenioides*, *P. tenuifolium* and *Coprosma lucida* J.R.Forst. G.Forst. grew together in a light gap in a single plot. These three species were also present in the sapling survey of this plot, indicating the ecological potential of some sapling species to attain canopy-level heights when conditions are favourable and a light gap occurs. Although the dominant canopy species were podocarps, these were predominately missing from the lower strata across all sites.

The structure of the midstorey in each fragment was variable, with intact remnants showing greater similarity in composition than the degraded site. Sapling counts resulted in averages for each site of 25 (Ōreti Road), 3800 (Fosbender) and 2800 (Daffodil Bay) per hectare (Table 1). Between the sites of Daffodil Bay and Fosbender, species composition in the sub-canopy was similar, with sapling counts dominated by *Pittosporum tenuifolium*, *Coprosma lucida* and *Myrsine australis* (A.Rich.) Allan. These three species accounted for 66% of total individual sapling records across the total study area.

In both the Ōreti Road and Daffodil Bay fragments, all sapling species were observed to be indigenous, although

Table 1: Comparison of different variables from the surveyed patches/sites.

Sites	Patch size (ha)	Species richness (species count)	Indigenous species richness (species count)	Indigenous dominance (%)	Sapling density (count)	Sapling density (per ha)	Understorey vegetation cover (%)	Woody seedling recruitment (individuals/plot)	Canopy cover
Ōreti Road	14	54	34	61	1	25	12.5	4.4	Podocarp, closed
Fosbender	16	26	23	91	152	3800	85	2.5	Podocarp, closed
Daffodil Bay	72	31	31	100	112	2800	90	5	Podocarp, closed

Figure 5: Clockwise from top left: Ōreti Road site permanent plot with peg markers; Ōreti Road site with limited subcanopy and understorey; Daffodil Bay site with abundant hound's tongue (*Zealandia pustulata* (G.Forst.) Testo et A.R.Field subsp. *pustulata*) ground cover; and abundant subcanopy and ground cover at the Fosbender site. Photo: Jordon Traill, April 2023.

the Ōreti Road plots were characterised by the near total absence of a middle strata (a single *Podocarpus totara* was recorded in one survey at this site). The sapling counts in Fosbender showed elderberry (*Sambucus nigra* L.) present in three of the four plots and *Berberis darwinii* Hook. in one plot, the latter considered a pest plant under the Southland Regional Pest Management Plan (Environment Southland 2019).

Understorey plant communities showed a similar difference in saplings, with great divergence between the Ōreti Road site and the Fosbender and Daffodil Bay sites. An overall understorey cover of 12.5% was observed in Ōreti Road compared to the more intact Fosbender and Daffodil Bay sites (85% and 90% respectively) (Table 1). The Fosbender and Daffodil Bay sites' understorey vegetation was dominated by indigenous species of the genera *Asplenium*, *Astelia*, *Lomaria* and *Zealandia pustulata* (G.Forst.) Testo et A.R.Field subsp. *pustulata* (Figure 5). The Ōreti Road plots had forest floors dominated by litter with limited but diverse non-indigenous grass and forb species, and indigenous sedge and fern species (Figure 5).

The Ōreti Road plots showed limited recruitment of woody species in the understorey, with an average of 4.4 woody seedlings per plot, the species here dominated by *Coprosma propinqua*. Additionally, this site showed *Podocarpus* sp. in the seedling counts, whereas the other two sites did not.

At Daffodil Bay an average of five woody seedlings were identified within each plot, consisting predominately of *C. lucida*. The Fosbender site had the lowest woody seedling recruitment at the understorey level (below 1.35 m), with an average of 2.5 woody seedlings recorded in each *Coprosma rotundifolia*-dominated plot.

Discussion

The comparison between three patches of tōtara dune forest along a degradation and fragmentation gradient revealed three key findings. The difference in species guilds between Ōreti Road and the reference sites was significant – many species, especially functional groups of broadleaf mid-canopy species and ferns, were absent at the Ōreti Road site; while the two reference sites, although of similar ages and management histories, had a different guild of species, predominantly belonging to the mid-canopy broadleaf functional groups. These findings contribute to a broader knowledge of forest ecology, and can aid in the development of effective conservation and management strategies for this rare and unique forest association.

Across all sites, tōtara was rare in the seedling and sapling counts – indicating minimal recruitment. Bergin et al. (2008) have shown that browsing of tōtara is extremely likely in areas where common brushtail possums (*Trichosurus vulpecula* (Kerr. 1792)) are present, which impacts the species' vigour and seed production. Norton (2000) states that tōtara is a light-demanding species and therefore becomes more abundant as seedlings in the understorey once a gap opens in the canopy that allows increased light to penetrate. Limited recruitment of tōtara seedlings could be due to the herbivory of introduced mammals, or it could be a natural phenomenon in local forest succession. Possum control, as is being carried out in the Ōreti Road site, would be anticipated to benefit seedling availability and survival, and investigation could take place after sustained possum control to gauge the impact of such a pest on tōtara regeneration.

Site differences

The surveys uncovered differences in mid-canopy species composition between the two reference sites, which indicates the importance of choosing multiple sites as reference points to inform ecological restoration management. The results show that six mid-canopy species occur across both reference sites and likely represent important species in Southland tōtara dune forests. *Myrsine australis*, *Aristotelia serrata*, *Coprosma lucida*, *Pittosporum tenuifolium*, *P. eugenioides* and *Pseudopanax crassifolius* (Sol. ex A.Cunn.) K.Koch are suggested as target species for restoration planting to best match nearby ecological processes (Table 2). Alongside these, *Podocarpus laetus* and *P. totara* are suggested for plantings on forest edges and within light gaps of existing tōtara dune forests.

Species absence from the Ōreti Road site could be attributable to deviated biotic and abiotic processes, primarily introduced species herbivory as well as hindrance of seed dispersal agents, depletion in the soil's seed bank and changes in climate (Allen et al. 2013). All six of these species have been recorded as being bird-dispersed in contemporary Te Waipounamu / South Island forest remnants (Wyman & Kelly 2017; Burrows 1994). Alongside this, skinks are likely present at the sites and may contribute to seed dispersal; although, in the Murihiku / Southland context, this role is somewhat understudied (Spencer et al. 1998). These six mid-canopy species could be monitored as potential indicators of restored ecological pathways and measures of management success for the Ōreti Road restoration site.

Differences in vegetation between the sites could be based on a combination of dune age, physiography, hydrological regime, and histories of disturbance and isolation. The creation of dune forests is a result of formation of soil above the sand over time without new sand ingress (Turner et al. 2012). The dunes at the Fosbender site are much older than those at the Daffodil Bay site (Norton 2000). A cause of the mid-canopy difference in the two reference sites could relate to the age of the dunes themselves, with carbon and nitrogen content expected to increase with increasing dune age (de Kovel et al. 2000). Additional research into dune age, topographical features, soil moisture levels, plant community composition and historical land use of the area would help identify factors influencing cross-site species differences.

Harding (1999) has shown that, along with dune age, the physiography of sites in these ecosystems plays an important part in the extant vegetation assemblages, and this impacts plot comparability. Through our choice of method, we attempted to rectify this; however, differences in aspect and light availability further impacted the composition of sites. For example, one of the plots from the Ōreti Road site extended into a diverse, damp dune hollow, which we did not try to replicate in the reference sites. Also, seasonal variations meant that some plant species, especially indigenous orchids (*Corybas* spp., *Pterostylis* spp.) that are found only in sites measured during spring, are not observable year-round although likely present at all sites. This means that limited comparisons could be made between annual or winter-dormant species in this study.

Despite the reduced sample size, the use of

Table 2: Suggested species for replanting and monitoring for restoration success.

Species	Te reo Māori and English names	Location*	Observed as canopy species	Dispersal modes
Aristotelia serrata (J.R.Forst. et G.Forst.) W.R.B.Oliv.	Makomako / wineberry	D, F, O	No	Birds
Coprosma lucida J.R.Forst. et G.Forst.	Karamū / shining karamū	D, F, O	Yes	Birds
Myrsine australis (A.Rich.) Allan	Māpou / red māpou	D, F	No	Birds
Pittosporum eugenioides A.Cunn.	Tarata / lemonwood	D, F, O	Yes	Birds
Pittosporum tenuifolium Gaertn.	Kohūhū / black matipo	D, F, O	Yes	Birds
Podocarpus laetus Hooibr. ex Endl.	Tōtara kōtukutuku / Hall's tōtara	D, F, O	Yes	Birds
Podocarpus totara G.Benn. ex D.Don var. totara	Tōtara / tōtara	D, F, O	Yes	Birds
Pseudopanax crassifolius (Sol. ex A.Cunn.) K.Koch	Horoeka / lancewood	D, F	No	Birds

* D: Daffodil Bay; F: Fosbender; O: Ōreti Road.

spatially distributed plots and standardised methods allows for cautious yet meaningful inferences about forest structure. Such a methodology mitigates some limitations associated with smaller datasets by ensuring that observations capture a range of variability across the landscape. However, to enhance the robustness and representativeness of future research, studies should incorporate full-plot sampling whenever feasible. Alternatively, if resource constraints persist, adopting well-designed random subsampling protocols can provide a reliable means of maintaining data quality and relevance between remeasures.

Natural recruitment in Ōreti Road

At the Ōreti Road site, the mid-canopy contains almost no saplings, and no angiosperms were recorded in the forest strata. A comparable number of indigenous woody seedlings were recorded between restoration and reference sites. Stock had been removed from the restoration site, and this release from grazing or trampling pressure may have led to this phenomenon. While density of indigenous woody seedlings is high at Ōreti Road, it is almost exclusively *Coprosma propinqua*.

The rapid recruitment of *C. propinqua* in the Ōreti Road plots indicates a resilience in this ecosystem, and following subsequent measures in permanent plots set up and managed by the Trust, it will be worth establishing whether the indicator species we have identified return to the sites. The site's proximity to a *Coprosma*-dominated wetland may help explain the presence of this species on the forest floor.

Dispersibility of Aotearoa / New Zealand indigenous forest plants has greatly reduced due to diminishing populations of indigenous avifauna outside of areas with active trapping (Masuda et al. 2014). The capacity for the Ōreti Road site to naturally recruit species depends on dispersal agents carrying seed from nearby. All indicator species and potential target species for replanting are primarily bird dispersed. An increase in the overall number of birds, along with a higher proportion of indigenous species, which are more likely to disperse indigenous plants, will enhance the dispersal potential of these angiosperms (Wyman & Kelly 2017). To expedite the process, in-fill planting the existing forest with these species would catalyse ecological cycling of angiosperms through the attraction of fruit-eating species, which would in turn increase both local seed banks and the rate of dispersal of target plant species.

Ecological integrity and resilience

All sites displayed significant indigenous plant biodiversity, with Daffodil Bay showing the highest level of indigenous dominance. The Fosbender site harboured two woody ecological weeds, elderberry and *Berberis darwinii*, both of which require active control measures. Ongoing surveillance should be conducted regularly to assess their spread, with particular attention given to *B. darwinii*, as it may require more immediate and targeted management responses to prevent further invasion. The site maintains a comparatively high level of species richness in the understorey and shrub layer. The Ōreti Road site showed an understorey and subcanopy diminished in both species richness and cover. *Coprosma propinqua* was the only species recorded in the seedling counts at this site, while potentially invasive non-indigenous woody species remain absent.

Under the Ecological Integrity criteria of McGlone et al. (2020) and adapted using commentary by Bellingham et al. (2021), Griffiths et al. (2021) and Schallenberg et al. (2011), the Daffodil Bay site has "the full potential of indigenous biotic and abiotic features and natural processes are present sustainably", as specified in the New Zealand Environmental Reporting Act (2005), indicating its 'Enhanced' integrity. Fosbender is categorised as 'Maintained' as per the Act; i.e., "The potential of indigenous biotic and abiotic features and natural processes are mostly present with tolerable inclusion of naturalised species and processes." The Ōreti Road site in its current condition is considered 'Deteriorated' under the Act's definition, as "the potential of indigenous biotic and abiotic features and natural processes are deteriorated or absent with frequent inclusion of naturalised species and interrupted processes." This is expected to change over time as the site responds to release from grazing and ongoing conservation management activities.

Two plots at the Fosbender site bore populations of two ecological weeds, these plots being adjacent to neighbouring disturbed but regenerating ecosystems. *Berberis darwinii* is a managed pest in Southland, as reported by Wildlands (2022), but not recorded in any previous survey of the reserve (Invercargill City Council 2013), indicating a reduction in integrity for this site. At Ōreti Road, 22 naturalised plants were observed, which is unsurprising as the forest patches are severely fragmented, feature minor buffers on edges, and have experienced prolonged periods of disturbance and proximity to farmland and semi-rural development.

The Daffodil Bay tōtara forest patch is surrounded by indigenous broadleaf forest, creating a resilience buffer along the tōtara dune forest's edge. Norton (2000) suggests that patches of tōtara dune forest in Southland are required to have a breadth of at least 195 metres to ensure tōtara forest patches are resilient to windfall. This study shows both the patches that had weed incursions were less than 195 m in breadth, indicating that this theory of minimum patch size for tōtara dune ecosystems confers both for windfall resilience and weed incursion.

Conclusion

Climate change is predicted to increase the severity of weather events, impacting forest nutrient cycling and water availability, and alter disturbance regimes (González de Andrés 2019). Some mid-canopy species aid in recovery after disturbances by quickly emerging to fill the canopy and occupy light gaps, thereby minimising the impact of wind intrusion from above. To protect the remnant forest patch at Ōreti Road, encouraging species that have this ecological trait could serve to improve the resilience of the forest into the future. This study indicates that *Coprosma lucida*, *Pittosporum eugenioides* and *P. tenuifolium* have the potential to exist as canopy species within this ecosystem. The other three species identified for restoration planting can occur as canopy species in other ecosystem types, and all could be targeted for planting or supplementary seeding within the area, especially in areas of known canopy damage.

The Ōreti Road site has a large perimeter-to-size ratio, and with the significant impact of weeds and long history of browsing we anticipate it will regenerate slowly. Strategically planting in open areas, especially those facing wind, will help expand their core area and reduce the impact of disturbances to the canopy, potentially enhancing patch resilience over time.

This study provides a useful baseline for vascular plant species along a fragmentation gradient in remnant tōtara dune forest systems. It confirms the healthy state of the tōtara dune forest system within the Sandy Point domain and provides detail on plant species variation across fragments in dunes of different ages. Seedlings of tree species with important ecological roles are missing from the understorey of the Ōreti Road site and should be included in supplementary planting.

Data Accessibility Statement

Contact authors for access to the research data.

Author Contributions

Yannick Dorsman: Conceptualisation (equal); methodology (equal); investigation (equal); resources (equal); visualisation (equal); writing – original draft (lead); writing – review and editing (equal); project administration (equal).
Jordon Traill: Conceptualisation (equal); methodology (equal); investigation (equal); resources (equal); visualisation (equal); writing – review and editing (equal); project administration (equal).

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Appendices

Appendix 1: Plant lists from the three sites – Ōreti Road, Daffodil Bay and Fosbender Park.

Plants:	Indigenous/ Naturalised:	Ōreti Road	Daffodil Bay	Fosbender Park
Acaena juvenca B.H.Macmill.	Indigenous	√		
Acaena novae-zelandiae Kirk	Indigenous	√		
Agrostis capillaris L.	Naturalised	√		
Agrostis stolonifera L.	Naturalised	√		
Anthoxanthum odoratum L.	Naturalised	√		
Aristotelia serrata (J.R.Forst. et G.Forst.) W.R.B.Oliv.	Indigenous	√	√	√
Asplenium appendiculatum (Labill.) C.Presl subsp. *appendiculatum*	Indigenous	√	√	√
Asplenium bulbiferum G.Forst.	Indigenous		√	√
Asplenium gracillimum Colenso	Indigenous	√	√	√
Asplenium lyallii T.Moore	Indigenous		√	
Astelia fragrans Colenso	Indigenous		√	√
Astelia nervosa Hook.f.	Indigenous	√		
Austroblechnum penna-marina subsp. *alpina* (R.Br.) A.R.Field	Indigenous	√		
Berberis darwinii Hook.	Naturalised			√
Cardamine sp.	Naturalised[1]	√		
Carex horizontalis (Colenso) K.A.Ford	Indigenous	√		
Carex uncinata L.f.	Indigenous	√	√	
Cirsium vulgare (Savi) Ten.	Naturalised	√		
Claytonia perfoliata Donn ex Willd.	Naturalised	√		
Clematis paniculata J.F.Gmel.	Indigenous	√	√	
Clematis sp.	Indigenous	√	√	
Coprosma areolata Cheeseman	Indigenous	√	√	√
Coprosma colensoi Hook.f.	Indigenous	√		
Coprosma lucida J.R.Forst. et G.Forst.	Indigenous		√	√
Coprosma propinqua A.Cunn. var. *propinqua*	Indigenous	√	√	√
Coprosma rhamnoides A.Cunn.	Indigenous		√	
Coprosma rigida Cheeseman	Indigenous	√		
Coprosma rotundifolia A.Cunn.	Indigenous	√		√
Coprosma rubra Petrie	Indigenous		√	
Cordyline australis (G.Forst.) Endl.	Indigenous	√	√	

1 This specimen was identified to the genus level. It is likely to be non-indigenous, given the documented presence of *Cardamine hirsuta* L. and *C. flexuosa* With. in the surrounding area.

Corybas trilobus Rchb.f. agg.	Indigenous	√		
Crepis capillaris (L.) Wallr.	Naturalised	√		
Dactylis glomerata L.	Naturalised	√		
Dryopteris filix-mas (L.) Schott	Naturalised	√		
Fuchsia excorticata (J.R.Forst. et G.Forst.) L.f.	Indigenous	√	√	√
Fuchsia perscandens Cockayne et Allan	Indigenous	√		
Galium aparine L.	Naturalised	√		
Griselinia littoralis (Raoul) Raoul	Indigenous	√	√	
Holcus lanatus L.	Naturalised	√		
Hydrocotyle heteromeria A.Rich.	Indigenous	√		
Hypericum androsaemum L.	Naturalised	√		
Hypochaeris radicata L.	Naturalised	√		
Hypolepis ambigua (A.Rich.) Brownsey et Chinnock	Indigenous	√		
Jacobaea vulgaris Gaertn.	Naturalised	√		
Lobelia angulata G.Forst.	Indigenous	√		
Lomaria discolor (G.Forst.) Willd.	Indigenous		√	√
Lotus pedunculatus Cav.	Naturalised	√		
Muehlenbeckia australis (G.Forst.) Meisn.	Indigenous	√	√	
Mycelis muralis (L.) Dumort.	Naturalised	√		
Myrsine australis (A.Rich.) Allan	Indigenous		√	√
Neomyrtus pedunculata (Hook.f.) Allan	Indigenous		√	
Nertera villosa B.H.Macmill. et R.Mason	Indigenous	√		
Parablechnum procerum (G.Forst.) C.Presl	Indigenous		√	
Parsonsia heterophylla A.Cunn.	Indigenous	√	√	√
Pellaea rotundifolia (G. Forst.) Hook.	Indigenous			√
Pittosporum eugenioides A.Cunn.	Indigenous		√	√
Pittosporum tenuifolium Gaertn.	Indigenous	√	√	√
Poa imbecilla Spreng.	Indigenous	√		
Podocarpus laetus Hooibr. ex Endl.	Indigenous	√	√	√
Podocarpus totara G.Benn. ex D.Don var. *totara*	Indigenous	√	√	√
Podocarpus laetus Hooibr. ex Endl. × *Podocarpus totara* G.Benn. ex D.Don var. *totara*	Indigenous	√	√	√
Polystichum vestitum (G.Forst.) C.Presl	Indigenous	√		√
Prumnopitys taxifolia (Sol. ex D.Don) de Laub.	Indigenous	√	√	√
Pseudopanax crassifolius (Sol. ex A.Cunn.) K.Koch	Indigenous		√	√
Pseudowintera colorata (Raoul) Dandy	Indigenous	√	√	√
Pteridium esculentum (G.Forst.) Cockayne	Indigenous	√		
Pterophylla racemosa (L.f.) Pillon et H.C.Hopkins	Indigenous		√	
Pyrrosia eleagnifolia (Bory) Hovenkamp	Indigenous	√	√	√

Ranunculus repens L.	Naturalised	√		
Rubus fruticosus L. complex	Naturalised	√		
Sambucus nigra L.	Naturalised	√		√
Senecio minimus Poir.	Indigenous	√		
Solanum dulcamara L.	Naturalised	√		
Solanum laciniatum Aiton	Indigenous	√		
Stellaria parviflora Banks et Sol. ex Hook.f.	Indigenous	√		
Taraxacum officinale F.H.Wigg. complex	Naturalised	√		
Tropaeolum speciosum Poepp. et Endl.	Naturalised	√		√
Urtica sykesii Grosse-Veldm. et Weigend	Indigenous	√		
Veronica salicifolia G.Forst.	Indigenous		√	
Zealandia pustulata (G.Forst.) Testo et A.R.Field subsp. *pustulata*	Indigenous	√	√	√