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RESEARCH ARTICLE OPEN ACCESS

A Functional Assessment of Community Vulnerability to the Loss of Myrtaceae From Myrtle Rust

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Received: 27 June 2024 | **Revised:** 11 September 2024 | **Accepted:** 18 September 2024

Editor: Marion Pfeifer

Funding: This work was supported by New Zealand's Biological Heritage, Ngā Rākau Taketake project RA3.1.B. and the New Zealand Ministry of Business, Innovation and Employment's Strategic Science Investment Fund and Beyond Myrtle Rust project #C09X1806.

Keywords: *Austropuccinia psidii* | functional redundancy | functional similarity | invasive pathogens | *Kunzea* | *Leptospermum* | *Metrosideros* | New Zealand | tree diseases

ABSTRACT

Aim: Woody ecosystems provide critical ecosystem functions and services but are increasingly threatened as invasive pathogens spread globally. Myrtle rust, caused by *Austropuccinia psidii*, arrived in New Zealand in 2017 and infects at least 12 of 18 species in the susceptible Myrtaceae plant family. Among these are species of structural, successional and cultural importance. We aim to assess whether the functional consequences of Myrtaceae loss could be mitigated if co-occurring species with shared functional attributes are able to replace them.

Location: New Zealand (but with concepts and methodologies that apply globally).

Methods: Using a nationwide forest and shrubland plot data set, we assessed community vulnerability to the loss of Myrtaceae species by analysing proportional changes in average trait values when they are absent and produced spatial predictions indicating where species loss might have the greatest impact on community functionality. We then assessed whether compensatory infilling by co-occurring species would mediate community vulnerability.

Results: Forests and shrublands containing *Kunzea ericoides* and *Leptospermum scoparium* are highly vulnerable to their loss. Areas most vulnerable overall are the central and south-eastern North Island, north-eastern South Island and Stewart Island. For all species, compensatory infilling moderated the impact of their loss. However, if co-occurring Myrtaceae were unable to respond, possibly if they were also infected, community vulnerability almost always increased because infilling species had different functional attributes, compounding the functional impact.

Main Conclusions: Early successional woody plant communities and Myrtaceae-dominated old-growth forests are at most risk. Our spatial assessment of species-level functional impacts from myrtle rust will facilitate better-informed landscape-level responses. Management actions and monitoring can now be targeted to areas and communities at greatest risk of losing ecosystem-level processes.

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1 | Introduction

Tree diseases caused by non-native pathogens represent a major pressure facing woody ecosystems world-wide (Liebhold et al. 1995). While pathogens have always been a threat to forests, anthropogenic processes such as the international plant trade, forest fragmentation and degradation, and climate change have enhanced the rates and severity of infection, threatening long-standing forest communities and species conservation (Fisher et al. 2012; Trumbore, Brando, and Hartmann 2015; Williams et al. 2023). The chances of epidemics are greater when a pathogen is invasive and encounters a population of naïve hosts (van der Plank 1960). Notorious examples include Dutch elm disease in Europe and North America (Brasier 1991), ash dieback in Europe (Gross et al. 2014), chestnut blight in North America and Europe (Rigling and Prospero 2018) and *Phytophthora cinnamomi*, which has spread world-wide from its likely centre of origin in South-east Asia (Jung et al. 2017). Eradication is often not possible following incursion of a non-native pathogen, so alongside research designed to identify susceptible species and resistant genotypes (e.g., McKinney et al. 2014; Smith et al. 2020), it is important to identify forest communities that may be at risk. Species differ in their contribution to forest structure and function, which means community-level assessments are important so that the impacts from species loss can be estimated and quantified and appropriate management implemented.

Austropuccinia psidii, which causes myrtle rust, is an actively spreading invasive pathogen (Coutinho et al. 1998). Native to South and Central America, it affects the Myrtaceae, a large family of around 5500 woody plant species (Thornhill et al. 2015). Since the 1970s, myrtle rust has been spreading in southern hemisphere Myrtaceae-dominated forests (Carnegie and Pegg 2018). In 2017, myrtle rust was found in northern New Zealand, and within 12 months it had spread to the northern South Island (Beresford et al. 2018). It has been confirmed on 12 of New Zealand's 18 native Myrtaceae species (Beresford, Shuey, and Pegg 2020) and has severely infected two species of the endemic genus *Lophomyrtus* and *Metrosideros excelsa* (Beresford et al. 2019; Toome-Heller et al. 2020). The disease attacks young tissue, and susceptible Myrtaceae become unable to recruit (Sutherland et al. 2020) or recover from disturbance (Fernandez Winzer et al. 2019). Severe cases can result in tree death (Glen et al. 2007) and localised extinctions (Carnegie et al. 2016; Pegg et al. 2017), with at least one species in Australia driven to the brink of extinction in the wild (Fensham et al. 2020). Many Myrtaceae species are ecologically important in New Zealand (Jo et al. 2022), being prominent in early successions and providing abundant nectar for pollinators, which also supports the honey industry (Butz Huryn 1995; Newstrom and Robertson 2005), and many species dominate mature canopies and contribute substantially to forest biomass (Carswell et al. 2012; Mason et al. 2013; Paul, Kimberley, and Beets 2021). Many of these species have highly specific habitats and variable local dominance, and all susceptible species have few refugia outside the range of the disease (Jo et al. 2022; McCarthy, Wiser, et al. 2021).

Functional traits related to ecosystem processes and services (Pan et al. 2022; Pérez-Harguindeguy et al. 2013; Violle et al. 2007), scaled according to the dominance of the plant (following the mass ratio hypothesis; Grime 1998), can be used to predict the potential community-level impact of loss of Myrtaceae. Using vegetation plots and functional trait data, we can predict the 'functional departure' experienced following the loss of a species and subsequent compensatory growth of other species and use this to estimate the disease's impact (Hill et al. 2019). We note, however, that compensatory growth and infilling by co-occurring species may ameliorate or intensify the impacts (e.g., Stevenson et al. 2023).

The objectives of this study were to investigate the potential impact of myrtle rust on the functional structure of communities of natural forests and shrublands in New Zealand, assuming loss of Myrtaceae species. To achieve this, we calculate and map this potential impact using nationwide plot inventory, functional trait and environmental data. We consider the effects of losing individual Myrtaceae species and of compensatory infilling while accounting for possible infection of co-occurring Myrtaceae. These results will inform the myrtle rust response and provide a guide for similar exercises elsewhere, allowing management actions to be applied in a geographic and species-specific manner.

2 | Methods

2.1 | Vegetation Data

Our analysis employs vegetation inventory data from the Land Use and Carbon Analysis System and the National Biodiversity Monitoring and Reporting System, a network of 20 m × 20 m permanent vegetation plots at the intersections of an 8 km grid across all New Zealand native forests and shrublands (Bellingham et al. 2020; Holdaway et al. 2017). We used data from the most recently available measurement (2009–2014), removing nine plots with non-native Myrtaceae and Myrtaceae not identified to species level for a total of 1005 plots, 750 of which had one or more Myrtaceae species (Appendix S1: Figure S1-1). These plots included 16 of New Zealand's 18 native Myrtaceae species. We included only woody species in our analysis, which encompassed trees (including tree ferns), shrubs, lianas and mistletoes but excluded subshrubs.

On each plot, species were assigned cover values within each of up to seven fixed-height tiers (Hurst, Allen, and Fergus 2022). Species cover was recorded in cover class ranges using a modified Braun-Blanquet scale: <1%, 1%–5%, 6%–25%, 26%–50%, 51%–75% and 76%–100%. To derive a single species-level cover value for each plot, we summed cover-class midpoint values across all height tiers, assuming random overlap, following Fischer (2015). Subspecies-level identifications were reduced to the species level, and we treated *Parsonsia capsularis* and *P. heterophylla* as *Parsonsia* spp. because they are usually not identified to species level on plots (134/214 records not identified to species level). All *Kunzea* spp. records were combined to *Kunzea ericoides* (A.Rich.) Joy Thomps. following a recent revision to the genus in New Zealand (Heenan et al. 2023).

2.2 | Plant Functional Traits

Species-level functional trait values were compiled preferentially from local data sets (Grubb et al. 2013; Jo et al. 2022; Mason et al. 2010; McGlone and Richardson 2023; McGlone, Richardson, and Jordan 2010; Richardson, Allen, and

Doherty 2008; Simpson, Richardson, and Laughlin 2016). Missing trait values were filled, where possible, from the global TRY database (Kattge et al. 2020), which contributed 5.8% of total species trait values (0.3% weighted by abundance). Remaining gaps were filled with genus- (17.7% of total species trait values; 0.9% abundance weighted), family- (2.8% and 0.1%) and growth form-level (2.8% and 0.2%) mean values from the local data, in that order. Traits selected included all those used in a recent functional assessment of New Zealand plant families (Jo et al. 2022): leaf dry matter content, leaf nitrogen (N) concentration, seed mass, wood density, specific leaf area (SLA) and maximum height, with the addition of binary traits describing whether a species is self-supporting, insect pollinated or fleshy-fruited. These traits were selected due to their relevance to plant growth, reproduction and ecosystem function, while also maximising the number of organs (trait 'dimensions') to adequately capture species' form and function (Laughlin 2014; Pan et al. 2022). For example, seed mass, pollination mode and fruit type are associated with reproductive strategy; SLA and leaf N with photosynthetic capacity and leaf longevity; maximum height with potential lifespan and light competition; and wood density with resource investment strategy, longevity and decomposition rate (Pérez-Harguindeguy et al. 2013).

2.3 | Calculating Community Vulnerability to Loss

Community vulnerability to the loss of Myrtaceae was calculated following Hill et al. (2019). This was completed for Myrtaceae species present in > 3 plots (15/16 Myrtaceae species present on plots; Appendix S1: Table S1-1). The steps are described in detail in Figure 1 of Hill et al. (2019), but those authors include an additional step (their step 3, weighting traits by importance for ecosystem services), which we did not follow due to the risk of subjectivity in the process. This calculation was repeated for all Myrtaceae species/plot combinations.

1. For each plot, abundances and trait values were compiled for all species.
2. For each trait, values were standardised on a 0–1 scale, where 1 is the value of the target Myrtaceae species and 0 is the value of the species most dissimilar to the target. The average plot-level value of each standardised trait was then calculated by multiplying it by each species' proportional cover (abundance, see below), then summing across species. The standardised trait values for individual traits where then averaged out across traits into an overall standardised trait level for the plot.
3. The average standardised trait level for the plot was then recalculated based on three scenarios: (i) assuming total loss of the target Myrtaceae (i.e., switching its abundance to zero) and no compensatory infilling by other species; (ii) assuming total loss of the target, followed by compensatory infilling where all remaining species increase in proportion to their original abundance to fill the space left by the target; and (iii) assuming total loss of the target followed by compensatory infilling by non-Myrtaceae species only. This final scenario assumes that co-occurring Myrtaceae may also be affected by myrtle rust and therefore unable to increase in abundance in response to loss of the target. We also calculated community vulnerability without considering abundance to assess target species that may be functionally distinct but present at low abundance.
4. The final community vulnerability scores were calculated as the proportional difference in average trait values between the current community and the community following the loss of the species, as per the three scenarios in step 3. Higher values indicate that the loss of the target species results in a greater functional departure of the plot.

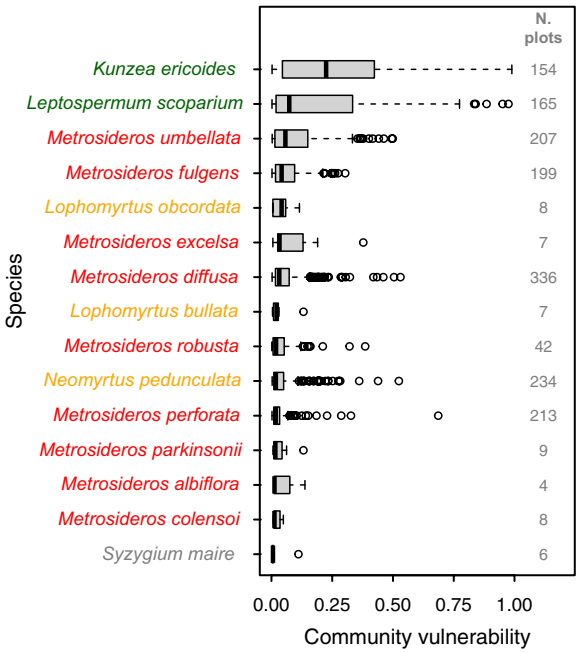


FIGURE 1 | Community vulnerability of plots to loss of Myrtaceae species (considering abundance, see Appendix S5: Figure S5-1, for vulnerability when not considering abundance) in New Zealand. Species are ranked based on their median community vulnerability. Species names are coloured based on their taxonomic tribe: green = Leptospermeae, red = Metrosidereae, orange = Myrteae, grey = Syzygieae (see also Table 1).

2.4 | Mapping Community Vulnerability

For each Myrtaceae species, we produced a map of community vulnerability to loss [assuming no compensatory infilling, scenario [i] above] using boosted regression trees (BRTs) (Elith, Leathwick, and Hastie 2008). Because we were unable to produce stable models for species present on < 30 plots, we could only produce community vulnerability predictions for 8 of the 15 Myrtaceae species considered (Appendix S1: Table S1-1). We also predicted the maximum community vulnerability from all Myrtaceae species present on a plot. We used a combination of environmental and remotely sensed layers as predictors (per Wiser et al. 2022), with environmental layers sourced from NZEnvDS (McCarthy, Leathwick, et al. 2021). Appendix S2 gives details of model construction and a list of all predictors.

We evaluated each model by examining the correlation coefficient between fitted and observed values, deviance explained

TABLE 1 | Boosted regression tree model parameters and model fit statistics.

Species	Tribe	Number of trees	Learning rate	Tree complexity	Correlation coefficient	Deviance explained
Kunzea ericoides	Leptospermeae	4650	0.001	2	0.61	0.29
Leptospermum scoparium	Leptospermeae	3950	0.001	1	0.33	0.16
Metrosideros diffusa	Metrosidereae	1950	0.001	2	0.38	0.16
Metrosideros fulgens	Metrosidereae	3350	0.001	1	0.18	0.10
Metrosideros perforata[a]	Metrosidereae	300	0.001	2	0.02	0.15
Metrosideros robusta[b]	Metrosidereae	—	—	—	—	—
Metrosideros umbellata	Metrosidereae	1450	0.005	4	0.36	0.14
Neomyrtus pedunculata	Myrteae	2850	0.001	2	0.42	0.23
Max. Myrtaceae community vulnerability	—	4000	0.001	3	0.57	0.25

[a]Community vulnerability maps were not produced for this species (correlation coefficient <0.1).
[b]Model did not converge.

in the training data set, and the relative influence of predictors, all from the final cross-validated model. We did not produce maps for species with correlation coefficients <0.1. Predicted community vulnerability maps were restricted to pixels/areas where each species occurs using published species-level distributions ($\geq 5\%$ probability of occurrence; McCarthy, Wiser, et al. 2021). For maximum community vulnerability, we restricted our predictions to those pixels/areas mapped as native woody ecosystems using the Land Cover Database (LCDB version 5.0; Manaaki Whenua – Landcare Research 2020), including the following classes: Broadleaved Indigenous Hardwoods, Indigenous Forest, Mānuka and/or Kānuka, Matagouri or Grey Scrub and Sub Alpine Shrubland.

3 | Results

In terms of abundance, communities were most vulnerable to the loss of *Kunzea ericoides* and *Leptospermum scoparium*, both in the Leptospermeae tribe (Figure 1; median abundance-weighted community vulnerability 0.23 and 0.07, respectively). Loss of *K. ericoides* in the northern and central North Island and in the north-eastern and interior of the South Island (Figure 2a; Appendix S3: Figure S3-1), had a severe impact, as did the loss of *L. scoparium* in the northern and central North Island, west coast and central South Island, and Stewart Island (Figure 2b; Appendix S3: Figure S3-2). Vulnerability to loss was proportional to each species' abundance (Appendix S4: Figure S4-1).

Communities were less vulnerable to the loss of Metrosidereae species than to Leptospermeae. When considering Metrosidereae only, was most vulnerable to the loss of the free-standing *Metrosideros umbellata* and the climber *M. fulgens* (Figure 1). Vegetation across most of the range of *M. umbellata* was vulnerable to its loss, especially Stewart Island (Appendix S3: Figure S3-13). Vegetation was most vulnerable to loss of the climber *M. fulgens* on the west coast of the South Island (Appendix 3: Figure S3-9). Maps for remaining species are presented in Appendix S3. Of the three species from the Myrteae tribe, communities were most vulnerable to the loss of *Lophomyrtus obcordata* (Figure 1). Communities with *Syzygium maire*, the single species in the Syzygieae tribe, were least vulnerable to the loss of a target Myrtaceae.

Without considering abundance, the highest community vulnerability to loss was from *M. excelsa* (Appendix S5: Figure S5-1). Vulnerabilities to the loss of *K. ericoides* and *L. scoparium* were still highly ranked. The two *Lophomyrtus* species dropped in their rankings, and *S. maire* remained the species with the lowest community vulnerability.

We had sufficient data to produce models for 8 of 15 Myrtaceae considered (Table 1; Appendix S1: Table S1-1). Most BRT models performed well, with correlation coefficients ranging from 0.33 to 0.61 for five of seven species (Table 1). The fit for the model for *M. perforata* was poor, so we did not produce a predicted community vulnerability map for this species, and the model did not converge for *M. robusta*, so we were able to provide predicted maps of community vulnerability for six Myrtaceae species. On average, summer: winter precipitation ratio had the greatest relative influence on the species-level models, followed by the normalised difference vegetation index (NDVI) and the enhanced vegetation index (Appendix S6: Table S6-1). Moisture stress index had the most influence on the maximum community vulnerability model, followed by NDVI. Partial plots showing how each predictor influenced the model are provided in Appendix S6: Figures S6-1–8.

Regions most vulnerable to the loss of Myrtaceae species collectively were in the central and south-eastern North Island, the north-eastern South Island and Stewart Island (Figure 3). Parts of inland Fiordland, the north-western South Island and the west coast of the North Island might be less vulnerable to the loss of Myrtaceae.

For all species, compensatory infilling by co-occurring species will moderate community vulnerability caused by the loss of the target species, especially the two Leptospermeae species

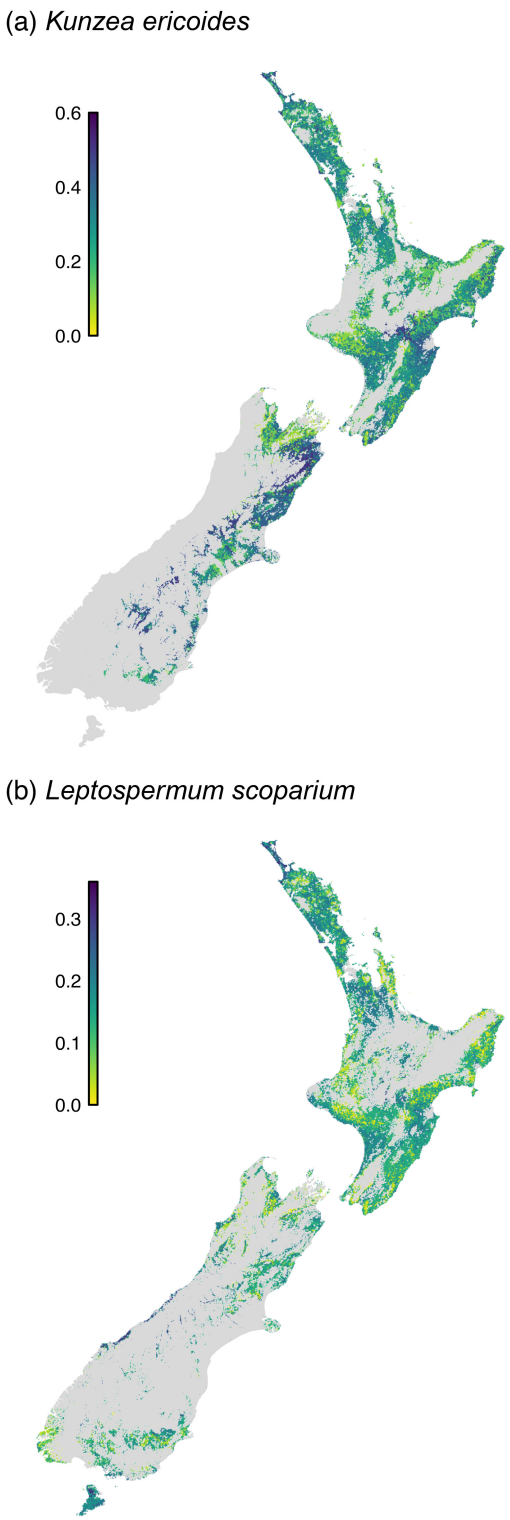


FIGURE 2 | Predicted community vulnerability to loss for *Kunzea ericoides* and *Leptospermum scoparium* in New Zealand. Higher values indicate greater community vulnerability to loss of each species.

(Figure 4). In most cases, however, vulnerabilities are even greater if co-occurring Myrtaceae are not able to respond with compensatory infilling and other co-occurring species respond instead, especially for non-Leptospermeae Myrtaceae tribes. This will take the community even further from its original state, especially if *M. parkinsonii*, *M. excelsa*, *M. perforata* and *L. obcordata* were lost (Figure 4).

4 | Discussion

Widespread loss of Myrtaceae from the invasive myrtle rust pathogen would cause substantial changes to the functional structure of New Zealand's forests. Our analyses report the highest community vulnerability score for two widespread, successional species–*K. ericoides* and *L. scoparium*–indicating that their loss would result in a considerable change in stand-level functional composition across a wide variety of locations. High community vulnerability to loss can arise because a species is locally dominant, limiting the capacity for co-occurring species to 'fill the gap' through the sheer amount of cover that would be required, even if they are functionally equivalent. Alternatively, the species' trait combination may be distinct from that of co-occurring species (e.g., Stevenson et al. 2023), a pattern common among subordinate and rare species in plant communities (Mouillot et al. 2013; Richardson et al. 2012). Our results do show, however, that compensatory infilling by co-occurring species could attenuate the impact of loss of individual Myrtaceae species, though community vulnerability often increased further if co-occurring Myrtaceae were unable to compensate, as may be the case if multiple taxa at a site become infected with myrtle rust.

4.1 | Vulnerability to Myrtaceae Loss

Around 10% of the once-forested areas of New Zealand are in successional shrublands, mostly dominated by *K. ericoides* and *L. scoparium* (Ewers et al. 2006; Wiser et al. 2011). Both species are wind dispersed, grow quickly (Russo et al. 2010), are browse-resistant (Forsyth et al. 2002) and widely distributed, being favoured by disturbance, in particular fire (Wardle 1991). While they are tolerant of exposure and have a wide edaphic range (including geothermal soils), *K. ericoides* prefers drier, warmer sites, whereas *L. scoparium* tolerates saturated soils, frost hollows and subalpine settings (Stephens, Molan, and Clarkson 2005; Wardle 1991). The northern North Island is most vulnerable to the loss of these species, as community vulnerability to their loss is high, and it is the area most suitable for myrtle rust infection (Beresford et al. 2018). Unless myrtle rust shifts towards cooler southern regions, areas such as Stewart Island, where *L. scoparium* is abundant, are unlikely to be affected.

Myrtle rust infection of *L. scoparium* occurs sparsely in the wild (though it has been observed on seed capsules indicating potential for disruption of regeneration; R. Beresford, pers. comm., 31/10/23), and not at all on *K. ericoides* (Beresford et al. 2019; Toome-Heller et al. 2020). Laboratory studies show that resistance and susceptibility are present in multiple tissue types (e.g., leaf, stem) of both species (Smith et al. 2020). New, more virulent myrtle rust strains could pose a risk (Soewarto et al. 2021), as could sexual recombination of the current pandemic strain (McTaggart et al. 2020, 2018), and increases in global change-driven disturbance events (e.g., Fernandez Winzer et al. 2019; Pegg et al. 2020). Pathogens causing widespread mortality of these species are not unprecedented. A notable example is *L. scoparium* infection from 'mānuka blight', caused by the native sooty mould *Capnodium walteri*, which feeds on honeydew produced by *Acanthococcus orariensis*,

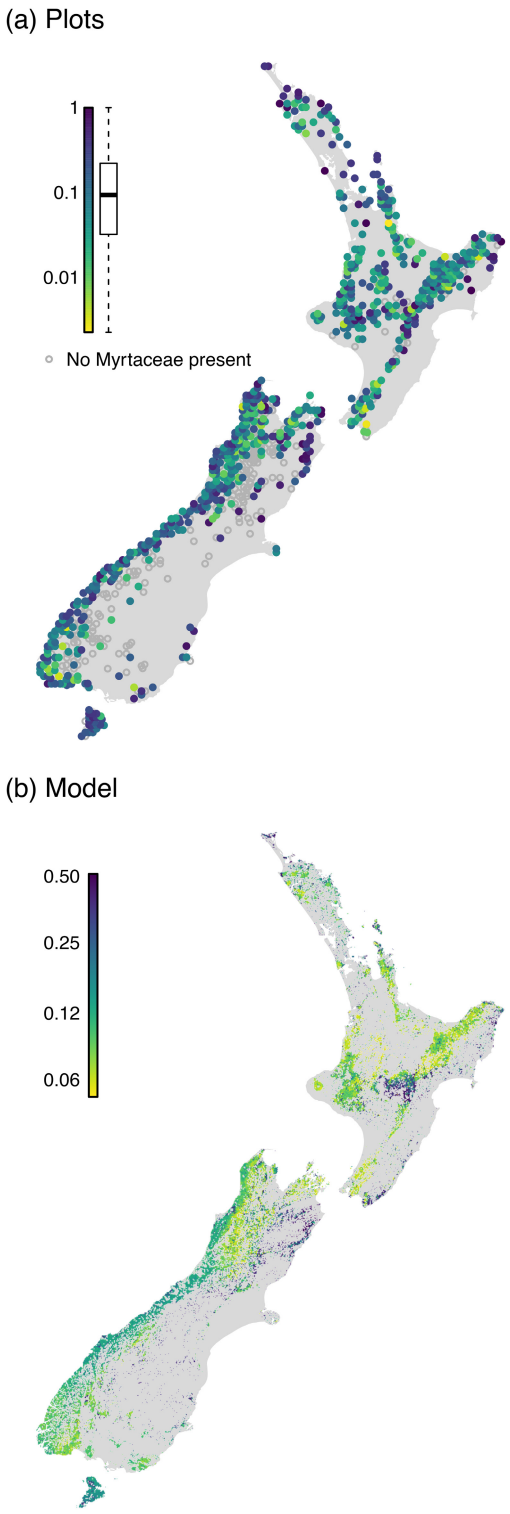


FIGURE 3 | Vulnerability to loss of the Myrtaceae species with the highest community vulnerability at the plot level (a), and (b) a prediction of maximum community vulnerability in New Zealand. Values are presented on a $\log_{10}$-scale in both panels.

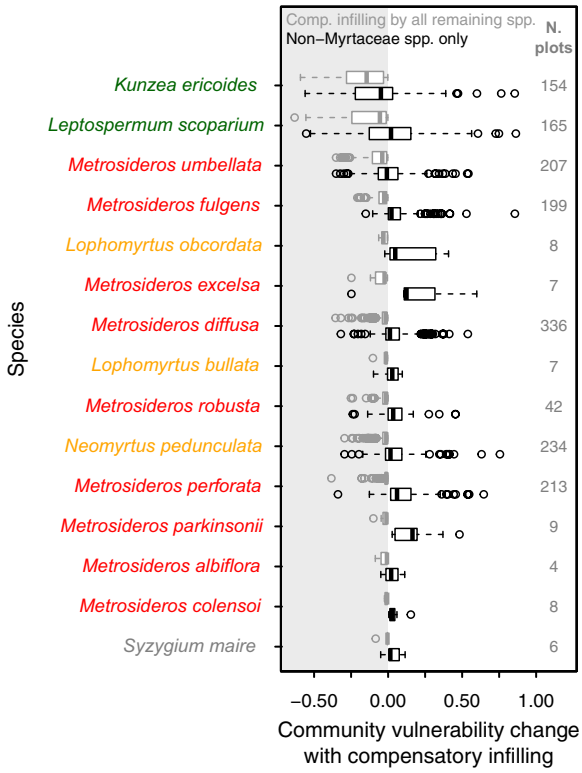


FIGURE 4 | The difference in plot-level community vulnerability to loss of Myrtaceae species with compensatory infilling by co-occurring species in New Zealand. We present community vulnerability change with (scenario [ii]; grey boxes) and without (scenario [iii]; black) allowing co-occurring Myrtaceae to respond. A negative change (grey-shaded area) means a plot is less vulnerable to a species' loss when co-occurring species infill to compensate. A positive change (unshaded) means infilling further increased vulnerability. Species are ranked based on their median community vulnerability from Figure 1. Species names are coloured based on their taxonomic tribe: green = Leptospermeae, red = Metrosidereae, orange = Myrteae, grey = Syzygieae (see also Table 1).

an Australian scale insect introduced sometime around 1937 (van Epenhuijsen et al. 2000). The blight also infects *K. ericoides* but only occasionally causes tree death (Hoy 1949). When the Australian scale insect was introduced, *L. scoparium* was considered a major pasture weed, so the disease was deliberately spread for control, but within 60 years the disease had declined (van Epenhuijsen et al. 2000).

Of the 12 species in the Metrosidereae, the highest community vulnerability relates to *M. umbellata* (when accounting for abundance; Figure 1) and *M. excelsa* (when not accounting for abundance; Appendix S5: Figure S5-1). Infection of *M. umbellata* is limited, and this species would be mostly spared due to its largely southern distribution (McCarthy, Wiser, et al. 2021). However, because of its capacity to form very large trees (diameters at breast height often > 2 m and heights up to 20 m) and its exceptionally dense wood (0.82 mg mm^{-3}) relative to other New Zealand woody species (mean = 0.55 mg mm^{-3}), the functional consequences of losing *M. umbellata* could be substantial. *Metrosideros umbellata* provides a key ecosystem service in its high carbon sequestration and its slow wood decomposition, in turn providing habitat for decomposers (Mason et al. 2013). On the other hand, its litter nutrient concentrations and decomposition rates are not different from dominant co-occurring trees (Bellingham et al. 2013), and neither are the decomposer communities that it supports in its litter (Wardle et al. 2006), in

which case its loss may not cause major changes in soil nutrient cycling. *Metrosideros excelsa* is considered particularly vulnerable to myrtle rust (Smith et al. 2020; Soewarto et al. 2021; Toome-Heller et al. 2020) and has limited potential refugia (McCarthy, Wiser, et al. 2021). It is primarily a successional species following disturbance (e.g., fire, landslide) and an early colonist on volcanic lava flows with its tough (SLA = 3.6 $mm^2 mg^{-1}$; New Zealand woody species mean = 10.05 $mm^2 mg^{-1}$) and nutrient poor (leaf N = 0.66% dry weight, mean = 1.41%) leaves promoting later successional species by forming a humus layer and altering the microenvironment beneath the plant (Bylsma, Clarkson, and Efford 2014; Clarkson 1990). This is analogous to the role of *M. polymorpha* in primary successions on lava flows in Hawai'i (Matson 1990). It dominates many small offshore volcanic islands, rocky coastal headlands and cliffs, but the grid-based national-scale plot data set used for this analysis poorly represents these ecosystems (Bellingham et al. 2020). Our results for this species are therefore informed by only seven vegetation plots, and conclusions as to community vulnerability may be underestimated.

Lophomyrtus bullata is a small tree that is patchily distributed primarily in forest margins and streamside vegetation (Allan 1961; McCarthy, Wiser, et al. 2021). It is the native species most affected by myrtle rust (Toome-Heller et al. 2020) and is represented in only seven vegetation plots in our analysis. Community vulnerability to the loss of *L. bullata* and the closely related *L. obcordata* and *Neomyrtus pedunculata* is moderate. Localised extinction is likely for *L. bullata* (Sutherland et al. 2020), and efforts are underway to assess the viability of preserving the species through ex situ conservation strategies such as seed banking (Nadarajan et al. 2021; van der Walt and Nadarajan 2023). Another highly susceptible species, *S. maire* (Schmid et al. 2021), is found mostly in lowland forests, usually on saturated soils. It currently occupies only a fraction of its natural range due to anthropogenic deforestation and land drainage (McGlone 1989). This species was lowest ranked in terms of community vulnerability, but it was represented by only six plots, and it is likely that none were sampled where it is dominant. Targeted studies of narrow-range and habitat-specific species such as *S. maire* (and *M. excelsa* and *L. bullata*) would be valuable to further understand the impact of their loss, potentially at scales more local than our national perspective. Additional traits, including further characterisation of the importance of various Myrtaceae to their associated biota (i.e., invertebrates; Sutherland et al. 2020), may also influence these results, though little is known of these interactions across the flora. For example, there may be some measure of synchrony of floral or fruit resource production relative to co-occurring species, and elements of nectar and fruit chemistry, given these four species (*Lophomyrtus* spp., *Neomyrtus* and *Syzygium*) are the only fleshy-fruited Myrtaceae in New Zealand. A feature of *S. maire* that is uncommon in New Zealand plants is the presence of pneumatophores, which enable it to dominate waterlogged soils. This could be another trait worth including in further studies targeting these habitat-specific species. Further studies could also consider alternate measures of functional redundancy (e.g., the impact on associated biodiversity; Mitchell et al. 2022) when considering the consequence of a species' loss.

4.2 | Compensatory Infilling

Compensatory infilling is likely to offset the functional impact following the loss of all 15 Myrtaceae species, but, crucially, only when co-occurring Myrtaceae can respond. If co-occurring Myrtaceae cannot respond (i.e., if they are also infected), compensatory infilling by non-Myrtaceae in most cases further increased community vulnerability scores. Differing susceptibility of co-occurring Myrtaceae species to myrtle rust (Toome-Heller et al. 2020) will influence their capacity to respond, and it will not be a simple matter of losses and gains of species. Furthermore, the rate at which co-occurring species will respond is unlikely to be equal, with a smaller pool of fast-growing species likely to be first in compensatory infilling.

Successional communities dominated by Leptospermeae often co-occur with non-native species such as *Ulex europaeus*, *Cytisus scoparius* and species of *Acacia*, *Hakea* and *Erica* (McQueen, Tozer, and Clarkson 2006; Wardle 1991). Given the dominance of *L. scoparium* and *K. ericoides* (e.g., Carswell et al. 2012; Nguyen et al. 2024; Scott et al. 2000), it is likely that compensatory infilling by non-native species will often occur. Some of these are functionally distinctive: *Acacia* spp., *U. europaeus* and *C. scoparius*, are nitrogen fixers (McQueen, Tozer, and Clarkson 2006), and all are fire-promoting. While they can facilitate succession (Lee, Allen, and Johnson 1986), the native forest resulting will be different from that via a Leptospermeae succession (Sullivan, Williams, and Timmins 2007). Compensatory infilling by these species could also reduce carbon sequestration and impact internationally agreed targets. Successional forests dominated by *K. ericoides* are significant carbon sinks owing to its tall stature (up to 25 m), high wood density (0.65 $mg\,mm^{-3}$) and long lifespan (up to c. 150 years; Burrows 1973). In contrast, shrublands dominated by *U. europaeus*, a likely replacement for *K. ericoides*, are significant carbon sources (Paul, Kimberley, and Beets 2021).

5 | Conclusions

In this paper, we show that widespread loss of Myrtaceae due to myrtle rust has the potential to substantially alter ecosystem processes in New Zealand's native woody systems. Successional processes seem most at risk, with the loss of the two Leptospermeae species predicted to have the most pronounced influence on ecosystem functional processes. Losing these landscape dominants could be analogous to the localised and functional extinction experienced in other pathosystems, including disease of ash, chestnut and elm populations in North America and Europe (Brasier 1991; Pautasso et al. 2013; Rigling and Prospero 2018). Fortunately, neither Leptospermeae is particularly susceptible to myrtle rust at present. On the other hand, highly susceptible endemic species (i.e., *L. bullata*, *L. obcordata*, *M. excelsa* and *S. maire*) are habitat specialists and make moderate to low contributions to site-level processes when ranked against other Myrtaceae. However, their patchy distribution and poor representation in our plot network mean further research is warranted. For example, *M. excelsa* exerts a strong influence in forest ecosystems on islands in northern New Zealand because its litter

is nutrient-poor, has high concentrations of phenolics, and decomposes more slowly than any co-occurring tree species (Wardle et al. 2009), so its loss from coastal and island forests may have profound consequences.

Our results provide guidance for where management actions would be best applied to reduce loss of ecosystem-level processes. Such analyses could also be applied to Australia and Hawai'i, which also have key dominant species susceptible to myrtle rust that could be lost from several key ecosystems (Fensham et al. 2020; Uchida, Zhong, and Killgore 2006). Fortunately, due to its recent arrival in New Zealand, the full impact of myrtle rust has not been realised, and it is still feasible to reduce the disease's potential consequences. Further, the risk of myrtle rust infection is low in cooler montane and southern coastal areas (Beresford et al. 2018), where susceptible species are unlikely to be affected (McCarthy, Wiser, et al. 2021). Possible management interventions include identifying and planting resistant genotypes (e.g., Silva et al. 2013; Sniezko 2006) and the application of chemical controls (e.g., Adusei-Fosu et al. 2021; Degnan et al. 2023). All likely management interventions are limited in their scale of application and will require prioritisation across susceptible species and spatial locations, but our research shows that targeted management applied to prevent location-specific species loss has substantial potential to reduce the overall functional impact of myrtle rust.

Author Contributions

J.K.M., S.J.R., I.J., S.K.W., T.A.E., and P.J.B. conceived the study and conceptualised the manuscript. J.K.M. and S.J.R. designed the methodology. J.K.M., S.J.R., I.J., and J.D.S. generated and collated the data. J.K.M. analysed the data and led the writing. All authors contributed to the drafts and gave final approval for publication.

Acknowledgements

We thank Ngā Rākau Taketake (project RA3.1.B) for funding this work. Additional funding was provided by the Ministry of Business, Innovation and Employment's Strategic Science Investment Fund and Beyond Myrtle Rust programme (#C09X1806). This analysis was partly based on data collected by the Land Use and Carbon Analysis System (Ministry for the Environment) and the National Biodiversity Monitoring and Reporting System (Department of Conservation), accessed from the New Zealand National Vegetation Survey Databank. We thank Angela Brandt for reviewing an earlier draft; Matt McGlone and Ray Prebble for editing; and Grant Smith and Rob Beresford for helpful discussions. The manuscript was improved following helpful comments from three reviewers.

Open access publishing facilitated by Landcare Research New Zealand, as part of the Wiley - Landcare Research New Zealand agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Vegetation plot data are archived in the National Vegetation Survey Databank, which can be accessed online at https://nvs.landcareresearch.co.nz by submitting a request using the plot IDs available on the Manaaki Whenua – Landcare Research DataStore: https://doi.org/10.7931/5yjq-mq83. The Myrtaceae spatial distributions are also hosted on the same repository.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13928.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.