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Ecological importance of the Myrtaceae in New Zealand's natural forests

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Abstract

Aims: The Myrtaceae is a woody family that plays an important role in forest ecosystems globally. The recent spread of myrtle rust, caused by a fungal pathogen (*Austropuccinia psidii*), from its native South America into New Zealand (NZ), highlights the need to quantify the ecological importance of Myrtaceae in NZ woody ecosystems.

Location: New Zealand.

Methods: Using NZ nationwide forest and shrubland inventory data, collected from 2009 to 2014, we quantified the ecological importance of Myrtaceae based on its richness and abundance relative to co-occurring woody families. We then explored how climate and forest stand structure affect Myrtaceae importance in general and by tribe and growth form. Finally, we compared functional traits associated with plant growth and reproductive strategies with other dominant woody families and determined Myrtaceae's contributions to community-weighted mean (CWM) trait values.

Results: Myrtaceae occurred in 74% of the study plots and its importance value was the second highest across the woody families. It was the only one in which climbers substantially contributed to the importance value (17%). Greater Myrtaceae importance values were associated with warmer and more mesic climates and early forest successional stages. Climate associations were similar within tribes and growth forms, whereas forest structure effects varied. Myrtaceae was functionally distinct from most co-occurring woody families. Contributions to CWM wood density, maximum height, and specific leaf area values were significantly greater than expected from its importance value.

Conclusions: Myrtaceae is the second most ecologically important woody family in NZ woody ecosystems. The family has a distinctive functional trait spectrum associated with high wood density and tall stature, ensuring large and enduring carbon stocks. There will potentially be large and deleterious outcomes in forest ecosystems if taxon-specific pathogens, such as *Austropuccinia psidii*, spread and significantly reduce Myrtaceae importance.

1 | INTRODUCTION

The Myrtaceae is one of the world's most species-rich flowering plant families (the seventh and 10th largest in the eudicot and vascular plant families respectively and the third largest tree family; World Flora Online, 2020), and is found throughout tropical, subtropical, Mediterranean, and temperate evergreen woody ecosystems (Mabberley, 2008). All species are woody and include climbers, small shrubs and trees, and emergent trees. The family provides resources for a wide array of organisms, including fungi, insects, birds, and mammals (Lindenmayer et al., 1991; McKenzie et al., 1999; Pizo, 2002; Affeld et al., 2009). It includes many species with cultural and economic importance (Abbott, 1992; Teulon et al., 2015). Myrtaceae trees are a relatively stable carbon store owing to their dominance and high wood density, which is associated with a slow decay rate after trees die (Chave et al., 2009; Kraft et al., 2010). The spread of a fungal pathogen specific to Myrtaceae, *Austropuccinia psidii* (the causal agent of myrtle rust), from its native South America poses a global threat (Coutinho et al., 1998). However, a quantitative, broad-scale assessment of the contribution of Myrtaceae to forest ecosystems in which they are common is lacking.

Myrtle rust arrived in New Zealand (NZ) in 2017 and is spreading (Teulon et al., 2015; Beresford et al., 2018; Toome-Heller et al., 2020). It has infected 17 native Myrtaceae species, killed adult trees of one species and has spread well beyond its predicted climatic range (MWLR, 2020). In Australia, myrtle rust (present since 2010) has caused tree death in at least five genera, localized extinctions, and substantial ecosystem change (Carnegie et al., 2016; Pegg et al., 2017). Browsing by non-native brushtail possums (*Trichosurus vulpecula*) also threatens some NZ Myrtaceae tree species (e.g. *Metrosideros* spp.), particularly when coupled with drought (Leutert, 1988; Bellingham & Lee, 2006). Thus, there is an urgent need to forecast the ecological consequences of pest-mediated decline across Myrtaceae.

The native Myrtaceae in NZ includes four tribes (Leptospermeae, Metrosidereae, Myrteae, and Syzygieae), six genera, and 28 species of trees and woody climbers (Allan, 1961; de Lange, 2014; de Lange & Schmid, 2021) and are important in diverse forests and shrublands (Wardle, 1991; Wiser et al., 2011; Wiser & De Cáceres, 2013). For example, the canopy tree *Metrosideros umbellata* occurs from shoreline to above the treeline in high-rainfall zones in the western South Island, and colonizes primary seres such as moraines and landslides, but also dominates old-growth forests and can persist on nutrient-depleted soils (Wardle, 1977; Reif & Allen, 1988; Richardson et al., 2005; Mason et al., 2012). Other Myrtaceae species, especially species of *Kunzea* and *Leptospermum*, dominate seral vegetation across

diverse environments (Enright, 1989; Allen et al., 1992; Stephens et al., 2005), playing important roles in succession.

Using plot-based vegetation data from across NZ, coupled with functional trait data, we present a quantitative assessment of Myrtaceae importance relative to major co-occurring woody families to determine the potential impacts of myrtle rust. Specifically, we asked: (a) how important are Myrtaceae compared with co-occurring woody families according to richness, cover, and basal area; (b) how do climate and forest stand structure relate to Myrtaceae importance, and how do the patterns vary by tribe and growth form; (c) how do Myrtaceae species compare with co-occurring woody families according to functional traits (wood density, leaf nitrogen [N], specific leaf area [SLA], leaf dry matter content [LDMC], maximum height, seed mass) related to key ecosystem processes (Lavorel & Garnier, 2002; Laughlin, 2014; Reich, 2014; see methods for more information on the selection of the traits); and (d) what contributions do Myrtaceae make to community-weighted functional trait values relative to their importance, and to those of co-occurring families?

2 | METHODS

2.1 | Vegetation data

Vegetation inventory data were sourced from the Land Use and Carbon Analysis System and the National Biodiversity Monitoring and Reporting System, which monitor natural vegetation systematically across NZ using 20 m × 20 m permanent plots, located on intersections of an 8-km grid superimposed on land mapped as forests and shrublands throughout NZ's main islands (34–47° S, 166–178° E), excluding subtropical and subantarctic islands (Allen et al., 2003; Wiser et al., 2011; Bellingham et al., 2020). We used data from the most recent inventory collected from 2009 to 2014. We excluded three plots with non-native Myrtaceae species (*Eucalyptus nitens*, *Eucalyptus globulus*, and *Eucalyptus delegatensis*), resulting in a data set of 1,011 plots (Fig 1). For each woody species in each plot, we compiled species level cover estimates from six fixed-height tiers (see below) and computed basal area from measures of diameter at breast height for all stems ≥2.5 cm. Subspecies level measurements were elevated to species level. We combined all *Kunzea* spp. records as *Kunzea ericoides* sensu lato since most plot data predate a recent revision to the genus (de Lange, 2014), and because the new species are difficult to distinguish in the field and molecular analysis strongly suggests that they do not merit species status (Heenan et al., 2021). Similarly, all *Leptospermum* spp. from our inventory period are treated as *Leptospermum scoparium* sensu lato because they predate a recent revision recognising a new species (de Lange
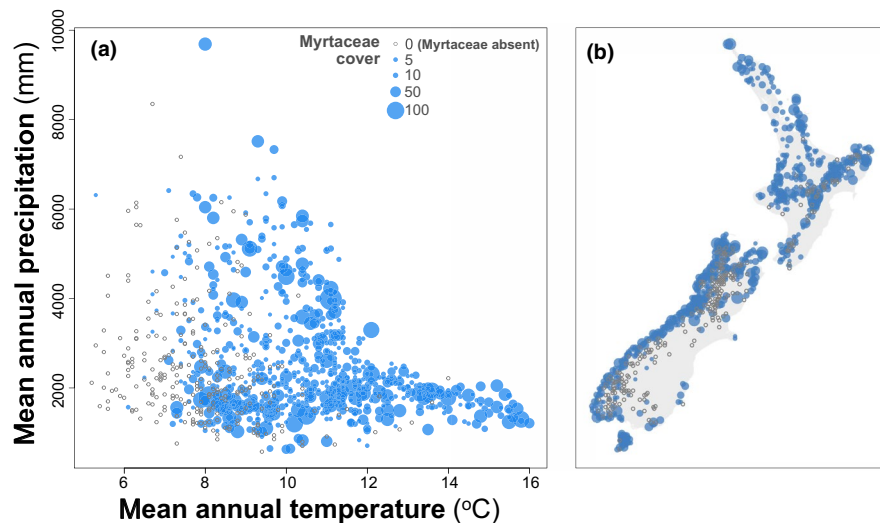
& Schmid, 2021). Woody species included trees (species reaching 6 m or more at maturity), shrubs (woody species <6 m at maturity), and lianas (including climbers), and arborescent herbaceous taxa that function as trees or climbers (a single palm species [*Rhopalostylis sapida*], four species of woody Asparagaceae [*Cordyline* spp.], eight species of tree ferns [*Cyathea* and *Dicksonia* spp.], and *Freycinetia banksii* [Pandanaceae]). Within each height tier, species cover was recorded using a modified Braun-Blanquet cover–abundance scale (1 = <1%, 2 = 1%–5%, 3 = 6%–25%, 4 = 26%–50%, 5 = 51%–75%, 6 = 76%–100%; Hurst & Allen, 2007). Species level cover values for each plot were calculated by combining species cover class midpoint values (%) across multiple height tiers assuming random overlap based on Fischer (2015). Identifications not resolved to the species level were found in 11 plots (basal area <1% of the total at each plot) and were removed from the data before analyses.

2.2 | Importance value

The importance values for woody families and Myrtaceae subgroups (tribes and growth forms) incorporate both cover and basal area measurements from the inventory data, following a modified method based on Mori et al. (1983). The importance value balances the species richness, cover, and stem basal area of a given taxon group relative to the total number of woody species, cumulative sum of all species cover values, and total basal area in a plot, and is expressed as a percentage importance:

basal area) that allows the dominance of trees to be considered. Overall species richness was calculated from the list of woody species in each plot.

2.3 | Plant traits

Functional trait values for the species present in the study plots were compiled primarily from NZ regional studies reporting the trait values (Richardson et al., 2008; Mason et al., 2010; McGlone et al., 2010; Grubb et al., 2013; Simpson et al., 2016). Missing traits for both Myrtaceae and common non-Myrtaceae species were measured wherever possible from additional field sampling in NZ natural forests, following Pérez-Harguindeguy et al. (2013), with any remaining missing values filled using the global TRY trait database (12% of total species trait values but representing only 1.7% when weighted by abundance; Kattge et al., 2020). The traits included LDMC (mg g^{-1}), SLA (cm^2 g^1), leaf N concentration (% dry weight), seed mass (mg), wood density (mg mm^{-3}), and maximum height (m). These traits were selected for their relevance to plant growth and reproduction, and ecosystem function (e.g. SLA and leaf N associated with photosynthetic capacity, seed mass with establishment success, maximum height with light competition, and tissue density [i.e. LDMC and wood density] with longevity and decomposition rate) (Pérez-Harguindeguy et al., 2013; Laughlin, 2014). NZ trait values were given precedence when calculating species level mean values, with values from TRY used if NZ data were absent.

$$\text{Importance}_{\text{group}}(\%) = \frac{\left(\frac{\text{Species richness in group}}{\text{Species richness}} + \frac{\text{Cumulative cover of species in group}}{\text{Total cumulative cover}} + \frac{\text{Basal area of group}}{\text{Total basal area}} \right)}{3} \times 100$$

Importance values based on richness, cover, and basal area are highly correlated with values based on richness and cover alone (Appendix S3). We used the importance values based on all three components because they account for climbers and shrubs without basal area measurements while retaining a measure of size (i.e.

For remaining trait data gaps, genus, family, and growth-form level mean values using NZ data were used, in that order of preference. Since Myrtaceae climbers (six *Metrosideros* species) can reach the top of canopy trees, the maximum height of the climbers was set at the maximum height of their tallest congener, *Metrosideros robusta*

(30 m). Community-weighted mean (CWM) trait values at the plot level were calculated by summing the trait values of recorded species weighted by their relative cover in the plot (Garnier et al., 2004). To assess the potential impacts of the loss of Myrtaceae on ecosystem functions, we calculated Myrtaceae contributions to CWM trait values relative to their importance value, by both taxon group and growth form, as a ratio of the sum of community-weighted trait values of species in the group of interest to CWM, subtracted and divided by the group importance value.

2.4 | Environmental variables

To determine the relationship between environment and Myrtaceae importance values, mean annual precipitation (MAP) and temperature (MAT) were extracted from spatial layers derived from weather data collected over the period 1950–1980 (Leathwick et al., 2002; McCarthy et al., 2021a).

2.5 | Statistical analysis

We determined how environmental variables and woody vegetation composition are associated with Myrtaceae importance using spatial models constructed via an integrated nested Laplace approximation (INLA) approach (Beguin et al., 2012; Lindgren & Rue, 2015). The INLA is designed to approximate Bayesian inference via flexibility in model structure (e.g. zero-inflated model) and rapid computation power, allowing spatial data analyses for large databases (Lindgren & Rue, 2015). Using the stochastic partial differential equation approach embedded in the R package *R-INRA* (Lindgren & Rue, 2015), we developed spatial models that incorporate spatial autocorrelation across all plots based on sparse precision matrices derived from a discrete indexed Gaussian Markov random field, formulated from the Gaussian field with Matérn covariance function and the triangulation of the study region with the geo-coordinates of the plots. The maximum edge size of the triangles was set to 15 km, with 10-km cut-off to capture smaller-scale autocorrelations in the models used in this study. Myrtaceae spp. were absent from 260 of 1,011 plots, so the importance values of Myrtaceae were zeros in these cases. To accommodate this, we modelled the probability of producing a structural zero as equal for all observations using the function "zeroinflatedpoisson1" implemented in *R-INLA* (Martino & Rue, 2009). Myrtaceae importance values (%) were rounded up to integers to fit the models with the Poisson distribution and to avoid reducing the values <1% to zero. Each response variable was modelled as a function of five predictor variables, which included climatic factors (MAP, MAT) and plot level forest stand structure variables (tree richness, density and basal area). All predictor variables were standardized to make the effect sizes comparable by subtracting the mean and dividing by 2 *SD*.

To compare multi-variate trait patterns of Myrtaceae with major co-occurring woody families (i.e. eight families whose importance

(a) **Familial importance value** (%)

(b) **Contribution to Myrtaceae importance by tribe** (%)
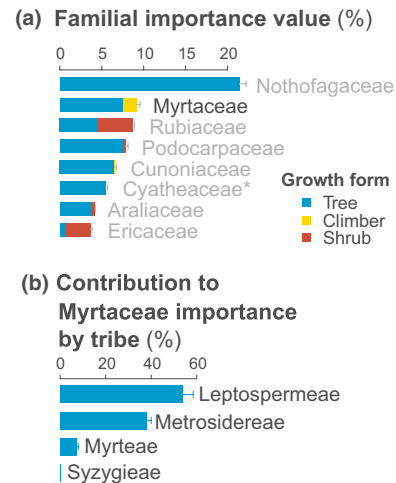
FIGURE 2 (a) Mean familial importance values of Myrtaceae and co-occurring woody plant families across the study plots in New Zealand forests and shrublands (*n* = 1,011). (b) Each tribe's contribution to Myrtaceae importance. Error bars are *SE* and families are ranked in descending order of their mean importance values across plots. Plot locations are shown in Fig 1b. Only those families in the top 10% quantile of families (eight families) based on the importance values out of total 71 are displayed. *Cyatheaceae is a tree fern family

value lies in the top 10% quantile of all families present in the plots) from the study plots, we performed a principal components analysis with the "prcomp" function in R 4.03 (R Development Core Team, 2020). We tested the significance of differences between species of Myrtaceae and each family using a permutational multivariate analysis of variance (PERMANOVA) with 100,000 permutations, implemented in the "adonis" function in R package *vegan* (Dixon, 2003).

3 | RESULTS

The Myrtaceae was the second most important woody family across NZ, with the second highest mean relative cover and basal area and the fifth highest mean relative richness (Fig 2, Appendix S2). Nothofagaceae had the highest importance, followed by Myrtaceae, Rubiaceae, Podocarpaceae and Cunoniaceae (Fig 2). Trees were the main growth form across all woody families, but only in Myrtaceae did climbers make a substantial contribution to their importance (17%; Fig 2).

Myrtaceae importance was positively associated with MAP and MAT but, at a tribal level, Leptospermeae was negatively associated with MAP, and Metrosidereae had no significant association with MAT (Fig 3). Trees and Leptospermeae had negative associations with tree richness and basal area and positive associations with tree density, in contrast to climbers and the other two major Myrtaceae tribes, Metrosidereae and Myrteae, which had weaker, positive associations with tree richness and tree basal area respectively (95% credible intervals overlapped with zero; Fig 3).
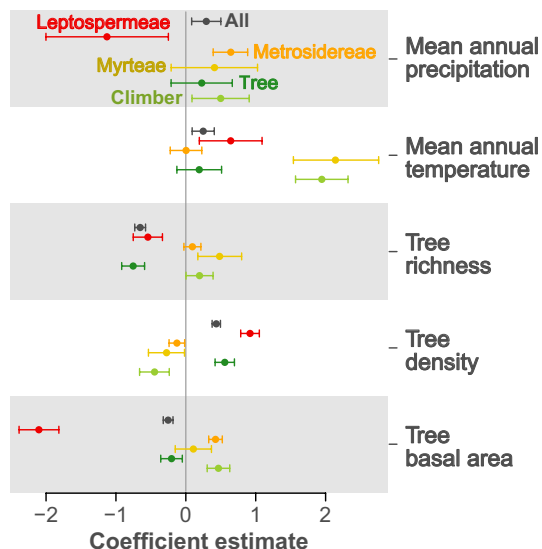
FIGURE 3 Climatic factors and forest stand structure associated with Myrtaceae (all) and Myrtaceae tribes' importance values across New Zealand forest and shrubland inventory plots. Coefficient estimates are based on zero-inflated generalized mixed effect models with spatial autocorrelation incorporated. Error bars are 95% credible intervals

The two primary axes of a principal components analysis of functional traits for species in Myrtaceae and seven major co-occurring woody families explained 57% of total trait variation (Fig 4). Myrtaceae occupied different regions of the trait space from other woody families ($p < 0.01$, PERMANOVA, Fig 4), except for Nothofagaceae and Cunoniaceae ($p > 0.1$, Fig 4). Overall, Myrtaceae were positively associated with wood density and maximum height, similar to Nothofagaceae and Cunoniaceae (Fig 4a, b, e, f). Myrtaceae species clustered into several subgroups along the PC1 axis, which relates to fast–slow plant growth strategies (high leaf N and SLA vs high LDMC; Fig 4b, e). Metrosidereae climbers, Myrteae species, and Syzygieae (*Syzygium maire*) were positioned towards the high leaf N and SLA end of this axis, and Metrosidereae trees and Leptospermeae species towards the other (Fig 4b).

Our comparisons of Myrtaceae contributions to CWM trait values relative to its importance value showed that Myrtaceae contributed significantly to CWM trait values for most functional traits, except for leaf N and LDMC (Fig 5, Appendix S1). Myrtaceae contributed 18% more for CWM wood density relative to its importance (Fig 5a). All tribes except Myrteae and the two growth forms had greater contributions to CWM wood density (Fig 5a inset figure). Myrtaceae contribution to CWM maximum height was 39% greater, despite Myrteae having 69% (±0.02 *SE*) less contribution to the CWM values (Fig 5b). For SLA, Myrtaceae contributed 10% more to the CWM values. Metrosidereae and Myrteae had greater contributions to CWM SLA values, but Leptospermeae had no significant difference (Fig 5c). CWM leaf N contributions by Myrtaceae tribes were no different from their importance values, but climbers contributed more and trees less to CWM leaf N (Fig 5d). Myrtaceae

contribution to CWM LDMC was not significant; however, at the tribal level, Leptospermeae contributed more and Metrosidereae and Myrteae less than their importance (Fig 5e). All Myrtaceae tribes and growth forms contributed significantly less to CWM seed mass than their importance (Fig 5f).

4 | DISCUSSION

Rapidly expanding global trade and climate change have increased the spread of novel pathogens in forest ecosystems (Liebhold et al., 1995; Anderson et al., 2004). In particular, the spread of tree pathogens with wide host specificity is of concern because multiple tree deaths can disrupt forest ecosystem structure and function (Grünwald et al., 2008; Ploetz et al., 2017). Our ability to forecast these impacts is limited by the lack of comparative analyses of woody species to test their relative importance and functional roles in the communities. Here we presented a novel framework for a quantitative assessment of woody families using systematic inventory data, incorporating community-weighted functional traits. We then applied this framework to determine the ecological role of Myrtaceae to assess the potential consequences of myrtle rust.

The Myrtaceae is a common, extremely diverse, and often dominant woody plant family (Raven & Axelrod, 1974; Thornhill et al., 2015) in tropical and southern hemisphere temperate forest and shrubland ecosystems. Myrtaceae is the second most important family in NZ forests and shrublands, following Nothofagaceae. Myrtaceae is more important than the Rubiaceae, Podocarpaceae, and Cunoniaceae — families that include some of the most common NZ tree and shrub species (*Coprosma* spp., *Dacrydium cupressinum*, and *Weinmannia racemosa* respectively; Fig 2). Of the three properties examined (species richness, cover, basal area), abundance (cover, basal area) contributed more than species richness to Myrtaceae's high ranking.

New Zealand Myrtaceae are therefore markedly different to those in East Asia, Australia, Madagascar, Amazon, and Brazilian Atlantic forests (Gentry, 1988; Alves et al., 2010; Laffan et al., 2013; ter Steege et al., 2013; Lucas & Bünger, 2015), where the family is important in basal area and cover but also highly diverse (e.g. on infertile soils in the Cerrado ecosystems of Brazil [Neri et al., 2012] and the lowland wet forests of eastern Brazil [Mori et al., 1983]). In Australia, Myrtaceae is the most diverse plant family, harbouring c. 1,600 species (Glen et al., 2007), over a quarter of the world's total of c. 5,500 species (Wilson, 2011). They are common and often dominant in rainforests, *Eucalyptus* forests (Tng et al., 2013), shrublands (Wills & Read, 2017), and wetlands (Fernandez Winzer et al., 2018). In contrast, in Hawai'i, Myrtaceae diversity is low (eight native species) and a single tree species (*Metrosideros polymorpha*) is the most abundant in forest ecosystems (Imada, 2012; Barton et al., 2021). Familial importance quantification of Myrtaceae has been reported for a lowland wet forest (Mori et al., 1983, only for trees) and Atlantic forests in Brazil (Lucas & Bünger, 2015, based on species richness) but we are unaware of any equivalent studies comparing
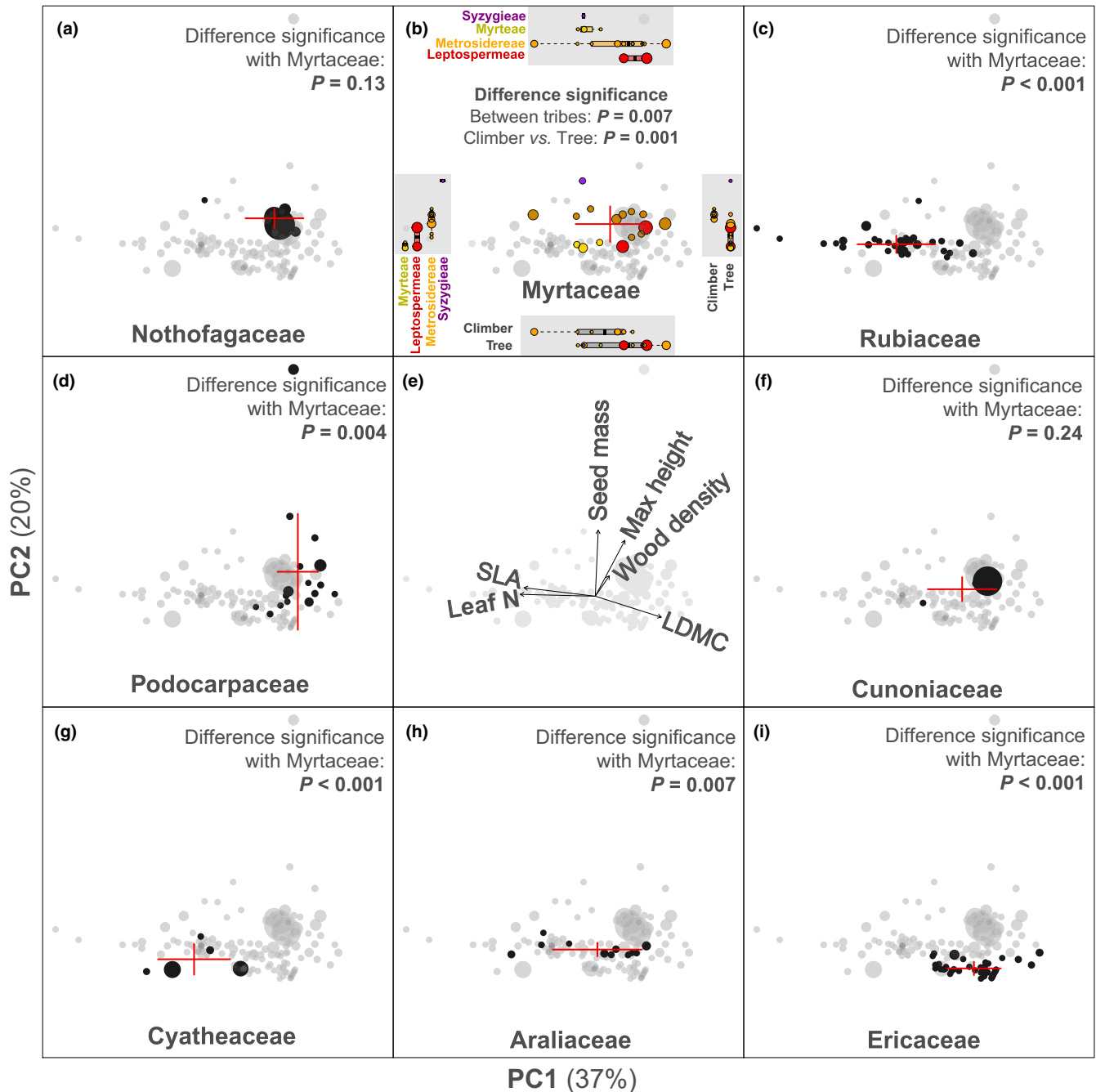
FIGURE 4 Principal components analysis of six functional traits across species of the top eight major woody families in New Zealand forest and shrubland inventory plots (see Fig 2a). Species scores along two major principal components are shown as grey circles, with size proportional to their mean cover across plots. Vectors representing the coefficients of the traits on the major two principal components are shown in (e). Contrasts with species in each family are presented as seperate panels (a–d, f–i). In these panels, centroids for each family (mean of species loadings with associated *SD*) are red and the circles of the species scores for that family are black. Significance of differences between species of Myrtaceae and each family and within Myrtaceae subgroups was tested using permutation tests for multivariate analysis of similarity (Dixon, 2003)

ecological importance of Myrtaceae with other co-occurring families using systematic inventory data of both richness and abundance, encompassing multiple woody communities across wide environmental gradients and including all woody growth forms.

Climbing species contribute significantly to the importance of Myrtaceae in NZ forests and shrublands. This is highly unusual

globally, since Myrtaceae species comprise, almost entirely, freestanding growth forms. A recent assessment of 38.6% of the global flora identified only eight of 1,893 Myrtaceae species (0.42%) as climbers (Taseski et al., 2019); of these, six are NZ endemic *Metrosideros* spp. The exceptional role of climbing Myrtaceae in NZ forests is underscored by their widespread occurrence (in 41%
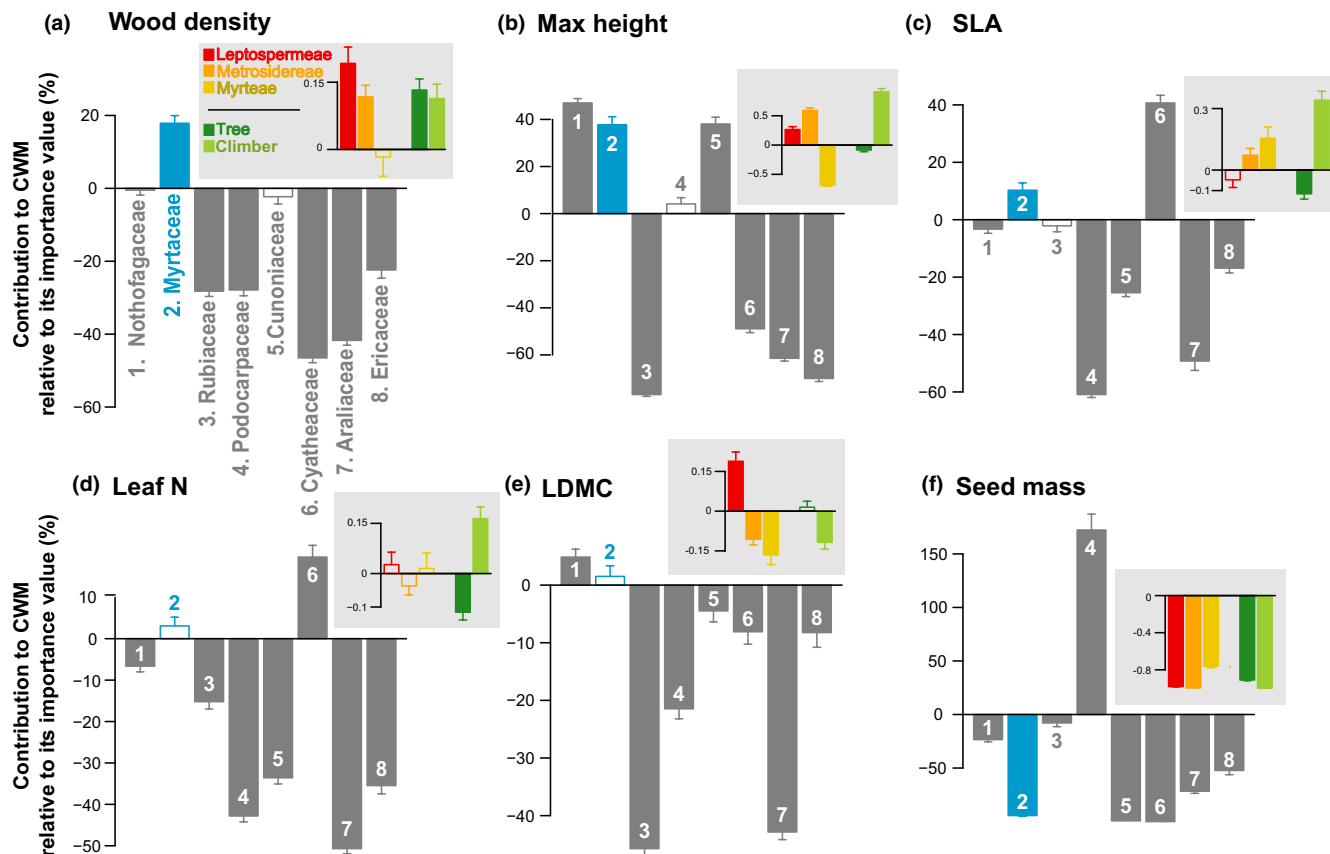
FIGURE 5 Family-level woody flora and Myrtaceae group contribution to community-weighted mean (CWM) trait values relative to their importance values in New Zealand forests and shrublands. Each group's contribution was determined as a ratio of the sum of community-weighted trait values of species in the group of interest to CWM, subtracted and divided by the group importance value. Only plots where the species in the group of interest was present were used in the analysis. Solid bars indicate a significant difference between the mean and zero based on a *t* test (alpha = 0.05). Error bars are *SE*. SLA, specific leaf area; LDMC, leaf dry matter content. Each group's contribution to CWM traits across entire plots is available in Appendix S1

of plots nationally [410 out of 1,011], especially in low-elevation [mean = 324 m asl, *SE* = 10] and high-rainfall [mean MAP = 2,613 mm, *SE* = 58] regions). To provide context, lianas (including climbers) of all families occur in 73% of plots nationally (743 out of 1,011), and the six *Metrosideros* climber species comprise nearly a quarter of NZ's 26 liana species distributed across nine families (Appendix S4). Accordingly, Myrtaceae was the only one of the eight major woody families to have a substantial representation by climbers (17% of its importance value, Fig 2 and Appendix S1). The unusual role of *Metrosideros* climbers in NZ forests may be due to their radiation into a niche globally occupied by climbing and strangling *Ficus* species, which are naturally absent from NZ (Dawson, 1967).

The divergent habitat characteristics of Myrtaceae tribes are associated with different forest stages. For example, Metrosidereae (four tree species and six climber species) and Myrteae (three tree species) are associated with high tree richness and tree basal area and low tree density, features associated with old-growth forests. In contrast, Leptospermeae, which includes two of the most common seral tree species in NZ (i.e. *Leptospermum scoparium* and *Kunzea ericoides* sensu lato), have stands with high stem densities, low species richness, and low basal area (Fig 3), representative of

the early-successional or disturbed stands typical of these species (Wardle, 1991; Allen et al., 1992).

Overall, greater Myrtaceae importance is associated with warm and mesic climates (McCarthy et al., 2021b). In this respect, the distribution of Myrtaceae in NZ is similar to that in other Pacific rainforests (e.g. Hawai'i), but contrasts with the dominance by Myrtaceae in seasonally dry ecosystems (e.g. *Eucalyptus* in Australia). Seasonally dry environments are limited in NZ and, where they occur (e.g. eastern NZ), are almost entirely deforested, and pollen records do not suggest past dominance by Myrtaceae (McGlone, 1989; Wilmshurst et al., 1997). The warm, oceanic climates of NZ are not only associated with a greater Myrtaceae importance, but also favour the spread of myrtle rust (Beresford et al., 2018; Narouei-Khandan et al., 2020). After the myrtle rust incursion, a cautious conservation approach was taken where all NZ Myrtaceae were considered vulnerable to myrtle rust and listed with a threatened status (de Lange et al., 2018), although we now know the degree of vulnerability differs among species (Smith et al., 2020; Sutherland et al., 2020; Soewarto et al., 2021). Warmer areas have a higher abundance and richness of Myrtaceae, adding to concerns that myrtle rust may have significant impacts on the conservation of at-risk species (Fensham

& Radford-Smith, 2021; McCarthy et al., 2021b) and the functional integrity of NZ ecosystems. The co-occurrence of relatively high Myrtaceae biomass and a climate that favours myrtle rust may also facilitate the spread of the pathogen through increased propagule pressure (Pegg et al., 2017).

Here we show that Myrtaceae have a suite of functional traits distinct from co-occurring major woody families. Within Myrtaceae, we found that trees and climbers have contrasting traits along the fast–slow continuum of plant strategies (Asner & Martin, 2012; Reich, 2014), suggesting divergent roles between growth forms in productivity, palatability, and nutrient cycling dynamics. For example, Myrtaceae climbers have traits associated with the fast end (e.g. high SLA and leaf N), whereas trees have low-quality leaf traits related to the slow end, consistent with other studies that found a faster growth strategy in lianas than in trees (Schnitzer & Bongers, 2002). However, compared with non-Myrtaceae lianas in NZ, Myrtaceae climbers have traits at the slow end of the fast–slow continuum (i.e. low SLA and leaf N) (Appendix S4). Their conservative trait spectra may explain their abundance (e.g. *Metrosideros diffusa*, *Metrosideros perforata*) in mature forests where light is limiting (Baars et al., 1998), and the positive association between Myrtaceae climber importance and mature forest (high tree basal area and richness but low tree density, Fig 3). It is an open question whether climbers, such as the NZ *Metrosideros* spp., differ in their functional traits and ecosystem function from other widespread climbers, especially lianas.

Among the eight most important woody families in our study plots, Myrtaceae made the greatest contribution to CWM wood density relative to its importance, underpinning its significance as a relatively stable carbon store since high wood density is associated with slow decay rates after trees die (Chave et al., 2009; Kraft et al., 2010; Mason et al., 2013). Similarly, high within-community wood density values (>1 mg mm^{-3}) are reported from Myrtaceae in montane tropical rain forests from Jamaica (two *Eugenia* spp. had the highest densities among 23 species sampled; Bellingham et al., 1995), and Thailand (two abundant species of *Syzygium* were in the top 15% of wood density values from a sample of 62 species; Sungpalee et al., 2009). While Myrtaceae often contribute high wood density to communities, this is not always the case; Tng et al. (2013) measured wood density among rainforest, savannah, and giant *Eucalyptus* forest communities in tropical and temperate Australia, and Myrtaceae had average wood density values, relative to co-occurring families in all community types. The greater contribution to CWM wood density relative to its importance is not only driven by tree species but also by climbers. Indeed, climbers contributed to the CWM wood density relative to their importance similarly to the tree species (Fig 5a inset figure). Although lianas are argued to have low wood density arising from their large vessel diameters servicing large leaves, and lack of standing structure (Putz, 1990; Schnitzer & Bongers, 2002), this may not apply to the relatively small-leaved *Metrosideros* climbers in NZ forests. Myrtaceae contributed 95% less and 45% more than its importance to CWM seed mass and maximum height respectively (Fig 5). An extensive literature review of seed size and associated life-history traits reported an "absence of long-lived,

small-seeded species" (Moles et al., 2004), but this combination is commonplace in Metrosidereae. Despite their small seed sizes (species mean ranged from 0.01 to 7.4 mg for NZ Myrtaceae, except for the larger-seeded *Syzygium maire* [133 mg]), NZ Myrtaceae trees can be long-lived (e.g. >1,000 years for *Metrosideros umbellata*, see Smith et al., 1985), which, when coupled with tall stature and high wood density, further reinforces their role as a stable carbon store in old-growth forests, and as a carbon sink during secondary successions dominated by Leptospermeae species (Carswell et al., 2012).

What would be the impacts of Myrtaceae decline or loss on process and function in NZ forest and shrubland ecosystems? No other NZ native family has the same combination of functional traits as Myrtaceae or makes a similar substantial contribution to the CWM of functional traits, so it is unlikely that any other native family could replace its function. Notably, no other family could replace the contribution by tall, high-wood-density Myrtaceae (e.g. *Metrosideros robusta*) to old-growth forest biomass and hence carbon storage. No other family contributes the trait spectrum of the Myrtaceae climbers. Moreover, Myrtaceae are functionally distinct in other ways we did not consider in this study; Myrtaceae flowers are often copious and sugar-rich, providing key resources for a diverse invertebrate and vertebrate fauna (Schmidt-Adam et al., 2000; Clearwater et al., 2021). Further, Myrtaceae includes two (i.e. *Kunzea* and *Leptospermum*) of only five NZ woody genera associated with ectomycorrhizal fungi, with most of the indigenous flora hosting arbuscular mycorrhizal fungi (Warcup, 1980; Orlovich & Cairney, 2004; Tedersoo et al., 2008). Collectively, the functionally distinct Myrtaceae with conservative traits linked to more closed nutrient cycling (Wardle et al., 2006, 2009; Mason et al., 2013) suggests that the decline of Myrtaceae species could potentially accelerate nutrient and carbon cycling, with large consequences for trophic networks. Secondary successions in eastern NZ are often dominated by Leptospermeae species (particularly *Kunzea*) resulting in tall, carbon-rich seral forests. Loss of Leptospermeae would have severe consequences for forest regeneration initiatives as the initial decades would instead depend on not only other native pioneer species (e.g. tree ferns and trees and shrubs of other families) but also non-native, often pyrogenic, shrub species that likely result in altered successional pathways (e.g. Sullivan et al., 2007; Brock et al., 2018; Wyse et al., 2018).

Vegetation assessment in forest ecosystems typically uses measures of tree stem counts and basal area, or foliar cover assessed using relevés. In the former approach, saplings and other growth forms (e.g. shrubs and climbers) are mostly disregarded unless they have a trunk structure similar to that of trees and their stem measurements (i.e. basal area) taken (Mori et al., 1983; Keel et al., 1993; Duivenvoorden, 1995). Using a systematic inventory data set that assessed vegetation using both structural and composition-based approaches, we demonstrated how these measures can be integrated to better quantify the relative importance of all plant growth forms, thus allowing us to better assess their ecological roles in forest ecosystems. The unique combinations of functional traits, and substantial contributions to CWM functional traits by Myrtaceae compared to co-occurring woody families in NZ forests and

shrublands, highlights the potential impacts of Myrtaceae loss due to the spread of myrtle rust. However, the effect of myrtle rust on forest community composition and ecosystem processes cannot be definitively predicted yet, due to unknown differences among and within species in their susceptibility to the pathogen (Smith et al., 2020; Soewarto et al., 2021) and gaps in species level functional trait values for a range of NZ species. Modelling potential shifts in forest community structure and community-level functional trait composition based on large-scale, long-term demographic studies allied with more comprehensive trait data that capture regional trait variation will improve our understanding of the functional roles of Myrtaceae, and the potential consequences of Myrtaceae loss in forest and shrubland ecosystems (Hill et al., 2019).

AUTHOR CONTRIBUTIONS

IJ conceived of the idea with input from PJB, TE, JKM, SKW and SJR. MP secured funding. JKM and SJR compiled functional trait data in New Zealand. IJ analysed the data and wrote the first draft. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The vegetation inventory data that support the findings of this study can be accessed by application to the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1 Importance values of dominant woody families and their contribution to community-weighted mean functional traits

Appendix S2 Metrics used for calculating importance values of woody families

Appendix S3 Relationships between importance values calculated based on richness, cover, and basal area and the values based on richness and cover

Appendix S4 Principal components analysis of five functional traits across native liana species (including climbers)