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RESEARCH ARTICLE

Historical land use couples with host density to affect myrtle rust impacts in a wet sclerophyll forest community in Eastern Australia

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Abstract

1. Non-native plant pathogens such as *Austropuccinia psidii*, the causal agent of myrtle rust, pose a significant threat to native forests. Myrtle rust is wind dispersed and its impacts are influenced by its ability to move through landscapes. Understanding the connection between land clearing processes and susceptible species dynamics is a crucial step towards developing targeted plant disease management strategies. We hypothesised that patches of wet sclerophyll forest with greater disturbance—particularly land clearing—would show higher densities of susceptible species in the subcanopy layer and therefore higher myrtle rust impacts.
2. To test this, we surveyed 21 patches of wet sclerophyll forest in eastern Australia, varying in land tenure and level of historical land clearing. We explored relationships between species abundance, susceptibility and myrtle rust impacts.
3. We found a positive interaction between historical land clearing, the abundance of susceptible species and myrtle rust impacts. Sites where susceptible species, particularly *Archirhodomyrtus beckleri*, were more abundant also showed more severe disease impacts.
4. *Practical implication*: Plant pathogens worldwide continue to spread outside of their native ranges into new habitats. Our results highlight the importance of investigating variable processes like land use legacy that can correlate with impacts of non-native plant pathogens. Our findings suggest that forest patches regrown after disturbance are more vulnerable to myrtle rust because of the composition of their subcanopy layer. Several management implications stem from our study. For example, formerly heavily cleared sites would benefit from monitoring for weeds that may establish in openings created by the death of susceptible trees. Less disturbed areas should receive targeted conservation to protect healthier individuals of species threatened by myrtle rust.

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KEYWORDS
Austropuccina psidii, disturbance, invasive species, land clearing

1 | INTRODUCTION

Non-native plant pathogens pose a key threat to native forests on their own; however, their impact can be either enhanced or diminished via interactions with other disturbance processes (Pautasso et al., 2010; Simler-Williamson et al., 2019). Whether a process selects for or against susceptible tree species is a key determinant of the direction and strength of a potential interaction with a pathogen (Simler-Williamson et al., 2019). For example, reduced fire frequency was associated with enhanced impacts of the plant pathogen *Phytophthora ramorum* in some forest patches in the southwest of the United States (Simler-Williamson et al., 2021). Patches that experienced less frequent fires since the 1950s were more likely to contain susceptible *Umbellularia californica* (Hook. & Arn.) Nutt. trees of a larger size, able to sustain high inoculum loads, increasing disease impact (Meentemeyer et al., 2008; Simler-Williamson et al., 2021).

Disturbance processes can also change the relative abundance and distribution of susceptible plants within a forest patch, which in turn can also influence disease impact (Burdon & Chilvers, 1982). For example, a higher density of susceptible trees has been associated with higher disease incidence and severity in forest patches affected by non-native plant pathogens *Hymenoscyphus fraxineus* in France or *Raffaelea lauricola* in the United States (Choudhury et al., 2021; Martin et al., 2025). A higher density of susceptible trees with high competence, the ability of an infected tree to transmit a disease, has been correlated with elevated inoculum loads in some studies, reflecting increased potential for transmission to other susceptible trees that are in close proximity (Dillon & Meentemeyer, 2019; Martin et al., 2025). However, in forests with multiple susceptible species, species can contribute unequally to these disease dynamics (Haas et al., 2016). An increased abundance of non-susceptible or low competence trees can dilute pathogen impacts. These trees can directly intercept passively dispersed spores, interrupting transmission between susceptible trees (Keesing et al., 2006).

Wet sclerophyll forests are transitional communities that are highly variable (Wardell-Johnson et al., 2017). These forests are characterised by an overstorey of sclerophyll species, often *Eucalyptus* or species from functionally similar genera, such as *Lophostemon* or *Syncarpia* (Wardell-Johnson et al., 2017). The subcanopy layer ranges from more open grassy shrub communities to more closed rainforest communities (Peeters & Butler, 2014). These forests are well adapted to fire, the frequency and severity of which is a key driver of the composition and structure of the subcanopy layer (Wardell-Johnson et al., 2017). Resprouting from basal or root buds is one trait that aids the long-term persistence of plant species in this forest type (Benwell, 2024), including several that are highly susceptible to myrtle rust, such as *Archirhodomyrtus beckleri* (F.Muell.) A.J.Scott and *Rhodamnia rubescens* (Benth.) Miq. (Benwell, 2024).

Wet sclerophyll forests are exposed to multiple threatening processes including altered fire regimes, land clearing and non-native plant pathogens. For example, altered fire regimes since European colonisation have been linked to increased recruitment of rainforest trees and complete transition to rainforest in some areas (Harrington & Sanderson, 1994). Clearing of forest for alternative land uses such as farming or housing is another threatening process. By the early 1980s, it was estimated that between 43% and 52% of tall and medium forests, including wet sclerophyll forests, in the state of Queensland had been cleared or highly modified (Wells et al., 1984). Land clearing remains a threat in Queensland with high clearing rates still recorded at around 114,000 ha/year of remnant vegetation in 2014–2015 (Reside et al., 2017). Non-native plant pathogens, particularly *Austropuccinia psidii*, the causal agent of myrtle rust, represent a further threatening process.

Myrtle rust is native to South America and was first detected in Australia in 2010 and has since spread rapidly (Carnegie et al., 2010; Pegg et al., 2014). The spores of the pathogen are primarily wind dispersed and affect young tissues (i.e. new leaves and stems) as well as the flowers and fruits of some species (Pegg et al., 2014). Susceptible species are concentrated in the Myrtaceae family, with over 380 confirmed hosts in Australia (Soewarto et al., 2019). Several highly susceptible rainforest species have experienced rapid population declines across their native ranges (Carnegie et al., 2016; Fensham et al., 2020), with 17 rainforest species predicted to become extinct because of the pathogen (Fensham et al., 2021, 2025).

Wet sclerophyll forests are particularly vulnerable to the impacts of myrtle rust. Rainforest trees are a key element of the subcanopy layer of wet sclerophyll forests in the subtropics, particularly patches in wetter and more fertile areas (Wardell-Johnson et al., 2017). As a result, myrtle rust impacts are concentrated in the subcanopy layer with the overstorey of the forest largely unaffected (Pegg et al., 2017; Stevenson et al., 2023). Several species that are known to be highly susceptible to myrtle rust, including *Rhodamnia rubescens* and *Rhodomyrtus psidioides* Benth. (Makinson, 2018), are characteristic of rainforest edge and transitional forest communities like wet sclerophyll forests (Floyd, 2008). High mortality rates of these and other susceptible species have already been recorded in patches of wet sclerophyll forest (Carnegie et al., 2016; Pegg et al., 2017). However, there are limited published data on how drivers, such as land clearing, affect the distribution and density of these species across the landscape.

We investigated several forest attributes associated with distribution and density of susceptible species that, in turn, may be associated with myrtle rust impacts at the patch scale. First, we investigated whether current land tenure representing different levels of human disturbance (i.e. national park, council or privately owned) was associated with myrtle rust impacts. We hypothesised that

land tenures associated with more anthropogenic disturbance, such as land clearing, would have a higher representation of early coloniser trees (e.g. *Archirhodomyrtus beckleri* and *Rhodamnia rubescens* (Benwell, 2024)) and therefore a higher potential for disease impact.

Second, we investigated whether historical land clearing (i.e. cover of native canopy trees in the 1960s) was associated with myrtle rust impacts via a difference in the density of key early coloniser species (e.g. *Archirhodomyrtus beckleri* and *Rhodamnia rubescens*). We hypothesised that sites that had experienced higher historical land clearing would have a higher representation of susceptible species, likely to be more prevalent in forests regenerating after disturbance.

Third, we investigated if the proportion of rainforest Myrtaceae trees was associated with the mean myrtle rust disease score in a forest patch. We hypothesised that the impact of myrtle rust on susceptible trees would be higher at sites where susceptible trees were at a higher density. In other forest communities, the incidence of myrtle rust was observed to be higher in patches where susceptible trees were more abundant (McCarthy et al., 2025).

Fourth, we investigated if forest edges would contain a higher representation of susceptible earlier coloniser species, as forest edges tend to be exposed to greater ongoing disturbance (Fox et al., 1997). Furthermore, as the spores of myrtle rust are primarily wind dispersed (Pegg et al., 2014), trees at the edges of patches may be more likely to be exposed to the spread of myrtle rust than trees inside the patch. For example, the transmission of wind-dispersed spores of the plant pathogen *Hemileia vastatrix* to the inner sections of agroforestry coffee systems can be reduced by rows of shade trees planted at patch edges (Avelino et al., 2023).

2 | MATERIALS AND METHODS

Data were collected from individual patches of a single forest community located at 21 different sites across the Southeast Queensland bioregion in subtropical Eastern Australia (Figure 1; Stevenson & Firn, 2026). The chosen forest community was wet sclerophyll forest with a rainforest subcanopy layer. At the 18 Queensland sites, the forest community was classified as Regional Ecosystem (RE) 12.11.2—*Eucalyptus saligna* or *E. grandis*, *E. microcorys*, *Lophostemon confertus* tall open forest on metamorphics ± interbedded volcanics (Queensland State Government, 2021) and, at the three sites in New South Wales, the equivalent Plant Community Type (PCT) 3172—Northern Ranges Brush Box-Flooded Gum Wet Forest (New South Wales, Department of Environment and Heritage, 2023). The latter community supports the same dominant canopy species as RE 12.11.2 and >80% of the characteristic tree and shrub species. As the Queensland mapping system is informed by underlying geology, only forest patches on

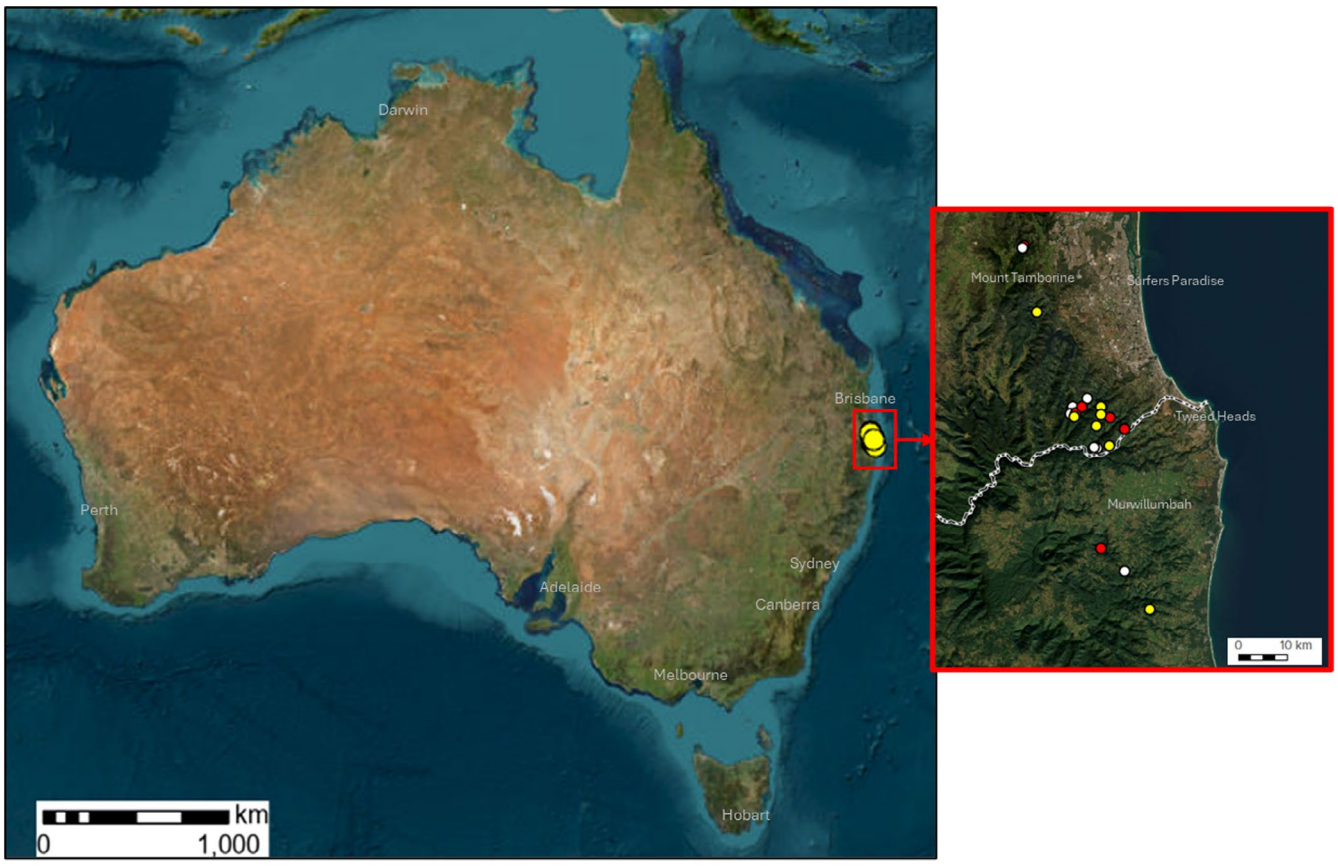


FIGURE 1 Map showing spatial spread of sampling sites across Eastern Australia. Sampling sites are marked with coloured circles indicating current land tenure: yellow—private, white—national park and red—council. Dashed lines represent state and territory boundaries.

metasediments were considered in New South Wales to ensure consistency between the states.

Sites were selected ensuring equal representation of the three current land tenures: private, council or National Park. Sites owned by the council or on National Parks were identified using online mapping programmes Queensland Globe and SEED map (Department of Natural Resources and Mines, Manufacturing and Regional and Rural Development, 2025a; New South Wales Government, 2025a). Privately owned sites were largely identified through local council staff and their contacts. Except for one privately owned site that has been the subject of monitoring for myrtle rust impacts since 2014 (Pegg et al., 2017; Stevenson et al., 2023), no knowledge of myrtle rust impact was sought prior to undertaking this study. This allowed us to investigate potential impacts of the pathogen generally and in an unbiased manner across this forest community. Approved research permits for our surveys were provided by Queensland Parks and Wildlife Service, New South Wales Parks and Wildlife Service, the Gold Coast City Council and the Tweed Valley Council. Written permission was given by private landholders allowing our surveys to proceed on their properties.

Historical aerial images for the region were downloaded from online repositories QSpatial and Historical Imagery (Department of Natural Resources and Mines, Manufacturing and Regional and Rural Development, 2025b; New South Wales Government, 2025b). Images were available from 1961 for 15 sites and from 1965 for the remaining six sites. These aerial images were compared to current satellite imagery from Queensland Globe and SEED map (Department of Natural Resources and Mines, Manufacturing and Regional and Rural Development, 2025a; New South Wales Government, 2025a). The start and end of transects were GPS tagged and plotted on current satellite images. These points and landmarks including waterways and roads were identified and matched between the images to determine the approximate location of the surveyed transects in the historical images. This method approximated the location of the three transects at each site, and then, the cover of native trees in each of these areas was estimated using two categories. Where native tree cover was absent (e.g. banana plantation) or sparse (i.e. >75% open canopy), sites were classified as having high historical land clearing ($n=4$). All other sites were categorised as having low historical land clearing ($n=17$).

At each site, three 50×2 m transects were established. Each transect was positioned to begin on an edge and end inside the patch of the target forest community. A diversity of edge types including pastures, main roads, walking tracks or forestry roads was included, as patches of the target forest community exist in a landscape with a diversity of land uses and levels of forest fragmentation. The first 10 m of each transect was marked as edge. The location of these transects was chosen to maximise their spacing within each patch of the target forest community, while also avoiding areas that were unsafe to traverse (e.g. steep drops or very steep slopes). Areas that had evidence of recent fire were also avoided, as this was not our target disturbance. This meant that the spatial arrangement of the transects varied between forest patches depending on the shape of the patch and the type of edge. All trees >1 m in height and <10 cm diameter at 50 cm height were recorded. These thresholds were selected to capture trees located in the mid/understorey layer (i.e. excluding seedlings and overstorey trees) as this is where most susceptible rainforest Myrtaceae species are found in this forest community (Pegg et al., 2017). Trees were identified to the species level, including those that had a dead main stem, and were resprouting from the base. Rainforest Myrtaecae trees (i.e. excluding eucalypt species) were tagged in our datasets to allow later investigation of potential differences in their representation of the total living trees between transects.

Variability in the distribution of species of differing levels of susceptibility to myrtle rust had the potential to mask patterns of disease impact. During our data collection, we observed that there was a distinct clustering of some susceptible rainforest Myrtaceae species between sites. The level of susceptibility and competence has been observed to influence disease dynamics in some forest systems (Rosenthal et al., 2021). This suggests that differences in the distribution of trees of differing susceptibility levels may also affect our results. To mitigate this risk, we categorised observed rainforest Myrtaceae species into two categories of susceptibility (high: 5 species or low: 6 species) using ratings collated by Makinson (2018) (Supporting Information S1). One species, *Syzygium oleosum* (F.Muell.) B.Hyland, was listed as having a wide susceptibility rating of relatively tolerant to highly susceptible (Makinson, 2018). It was rated as low susceptibility in this study based on field observations. Subsequent analyses were run including all rainforest Myrtaceae species and those of only high or only low susceptibility.

Myrtle rust impacts were estimated for each rainforest Myrtaceae tree using a method adapted from Fensham et al. (2021). This method assesses major branches, those extending from the central stem, and minor branches, those extending from the main branches. We determined the percentage of major branches on each tree that were dead (i.e. no living foliage remaining) and ascribed the appropriate category (0: 0%, 1: >0 to <10%, 2: 10 to <50%, 3: 50 to <90%, 4: 90 to <100% and 5:100% but resprouting from the base). We then estimated the percentage of minor branches that were dead, this included those attached to dead main branches and ascribed the associated category (0: 0%, 1: >0 to <10%, 2: 10 to <50%, 3: 50 to <90% and 4: 90%–100%). The mean of the scores associated with the two categories was then taken to assign a single disease score between 0 and 4.5 for each tree. A mean disease score per transect was then calculated by taking the average of these scores.

Myrtle rust has been present across the study region since 2011 (Carnegie et al., 2016; Pegg et al., 2014). We attempted to confirm the presence of the pathogen locally at sites during our surveys. Susceptible foliage on rainforest Myrtaceae trees in our transects was visually assessed for symptoms typical of myrtle rust (Pegg et al., 2014). Susceptible trees observed within eyesight of transects or while walking to or from study sites were also opportunistically searched for symptoms of myrtle rust. Damage not consistent with myrtle rust, likely caused by other pathogens or insects, was observed on three susceptible species *Acmena smithii* (Poir.) Merr.

& L.M.Perry, *Syzygium oleosum* and *Pilidiostigma glabrum* Burret (Supporting Information S2). This only reflected minor damage and was not scored as myrtle rust dieback when observed.

Data analysis was completed in R version 4.4.1 (2024-06-14) 'Race for Your Life' and Rstudio version 2024.4.2.764 'Chocolate Cosmos' (Posit team, 2024). Bayesian regression models were run using the brms package and Markov chain Monte Carlo sampling (Bürkner, 2017). Default priors specified by brms() were retained for each model as no informative priors were available. Models were set to 4000 iterations, with 2000 iterations as warmup. The number of chains and cores was set to 4. Convergence was checked visually and using Rhat values that each equalled 1. The seed function was specified to ensure repeatable results. Visual checks for model fit were conducted using forms of the pp_check() function from the brms package (Bürkner, 2017). The form selected for each model was determined based on the type of data (i.e. discrete or continuous data).

To test for evidence of a difference in the proportion of rainforest Myrtaceae trees between sites with differing levels of historical land clearing, current land tenure or proximity to the forest edge, Bayesian regression models were used. Models were run including all rainforest Myrtaceae species and then including only species categorised as having high or low susceptibility. Models were fitted with a random effect structure of transect nested in site to account for pseudo replication in the experimental design. While species area curves were used to check sampling sufficiency (Supporting Information S3), the low sample size at each site ($n = 3$ transects) created some issues of divergence in the models; the adapt delta value was increased up to 0.96 to correct these issues (Bürkner, 2017). Visual checks were conducted to check for issues of zero inflation and a comparison of fit made with a zero-inflated binomial distribution using the loo_compare() and loo() functions from the brms and loo packages (Bürkner, 2017; Vehtari et al., 2024). Zero-inflated binomial distributions were indicated and used in models that investigated an effect of forest edge and those that contained only highly susceptibility species. A standard binomial distribution was used in all other models.

Bayesian regression models were also used to determine evidence for a difference in mean disease score between sites with varying levels of historical land clearing, current land tenure or proximity to forest edge. Models were repeated using mean disease score data calculated with only high or only low susceptibility species. To meet assumptions of a beta distribution that requires values to be bounded between 0 and 1 (McCarthy, 2007; pg. 266–268), scores for each transect were divided by the maximum disease score of 4.5 to give a decimal proportion. After this transformation a single value of 1, representing the upper limit of the bounding, was present in datasets that contained all Myrtaceae species and only highly susceptible species. Therefore, a correction factor was applied to bring these values away from the upper limit of the interval (Smithson & Verkuilen, 2006). Defined as $(\text{score} * (n - 1) + 0.5 / n)$ where score represents the mean disease score for all rainforest Myrtaceae trees in a transect represented as a decimal proportion and n represents the number of rainforest Myrtaceae trees that were recorded in a transect. These datasets were used in all following models that contained disease score. This approach was selected over the use of a zero_one_inflated_beta distribution as no 0s were present, reducing potential issues of overfitting.

As our study was observational, and sites selected without prior knowledge of species composition, rainforest Myrtaceae trees were not present at all sites or in all transects. This meant a very low number of replicates ($n = 1$ transect) at some sites, creating issues of model fit when transect and site were specified as nested random effects. To mitigate this issue, only site was specified as a random effect in models that included disease score datasets.

Evidence for a correlation between the proportion of rainforest Myrtaceae trees and mean disease score was also tested using Bayesian regression models. Models were run including all rainforest Myrtaceae species and only those of high or low susceptibility. To meet the requirements of a beta distribution, counts of rainforest Myrtaceae trees were divided by the total count of living trees in a transect to represent a decimal proportion bounded between 0 and 1. Consistent with other models that contained mean disease score data, only site was specified as a random effect.

Estimates (median) and 95% credible intervals (CIs) of the posterior probability distribution are reported. Where CIs do not cross zero, effects are interpreted to have high probability of being credible or 'significant'. To aid interpretation, effect estimates were extracted from the posterior distribution of each model on the response scale using the add_epred_draws() function from the tidybayes package (Wickham, 2014). Estimates and 95% CIs from models containing mean disease score were multiplied by 4.5 to return values to the original scoring scale, while those from models containing the proportion of rainforest Myrtaceae were multiplied by 100 to give a percentage. Results were plotted using the ggplot2 and patchwork packages (Pedersen, 2020; Wickham, 2016).

3 | RESULTS

The effect of land tenure on the proportion of rainforest Myrtaceae trees is likely negligible, as indicated by the inclusion of zero in the 95% CIs (council and National Park: median = −0.10, 95% CI = −1.45 to 1.35, council and private: median = 0.49, 95% CI = −0.91 to 1.91, national park and private: median = −0.6, 95% CI = −2.01 to 0.82). Similarly, there is likely no meaningful effect of current land tenure on mean disease score (council and national park: median = −0.08, 95% CI = −1.32 to 1.18, council and private: median = −0.16, 95% CI = −1.41 to 1.10, national park and private: median = 0.08, 95% CI = −1.14 to 1.28).

There was a positive effect of historical land clearing on the proportion of rainforest Myrtaceae trees (median = 1.64, 95% CI = 0.53 to 2.76). Sites that experienced high historical land clearing had a higher proportion rainforest Myrtaceae at 16% (95% CI = 6%–34%) compared to 4% (95% CI = 2%–6%) at sites that experienced low historical land clearing (Figure 2a). The high posterior probability for a positive effect was maintained when only highly susceptible species

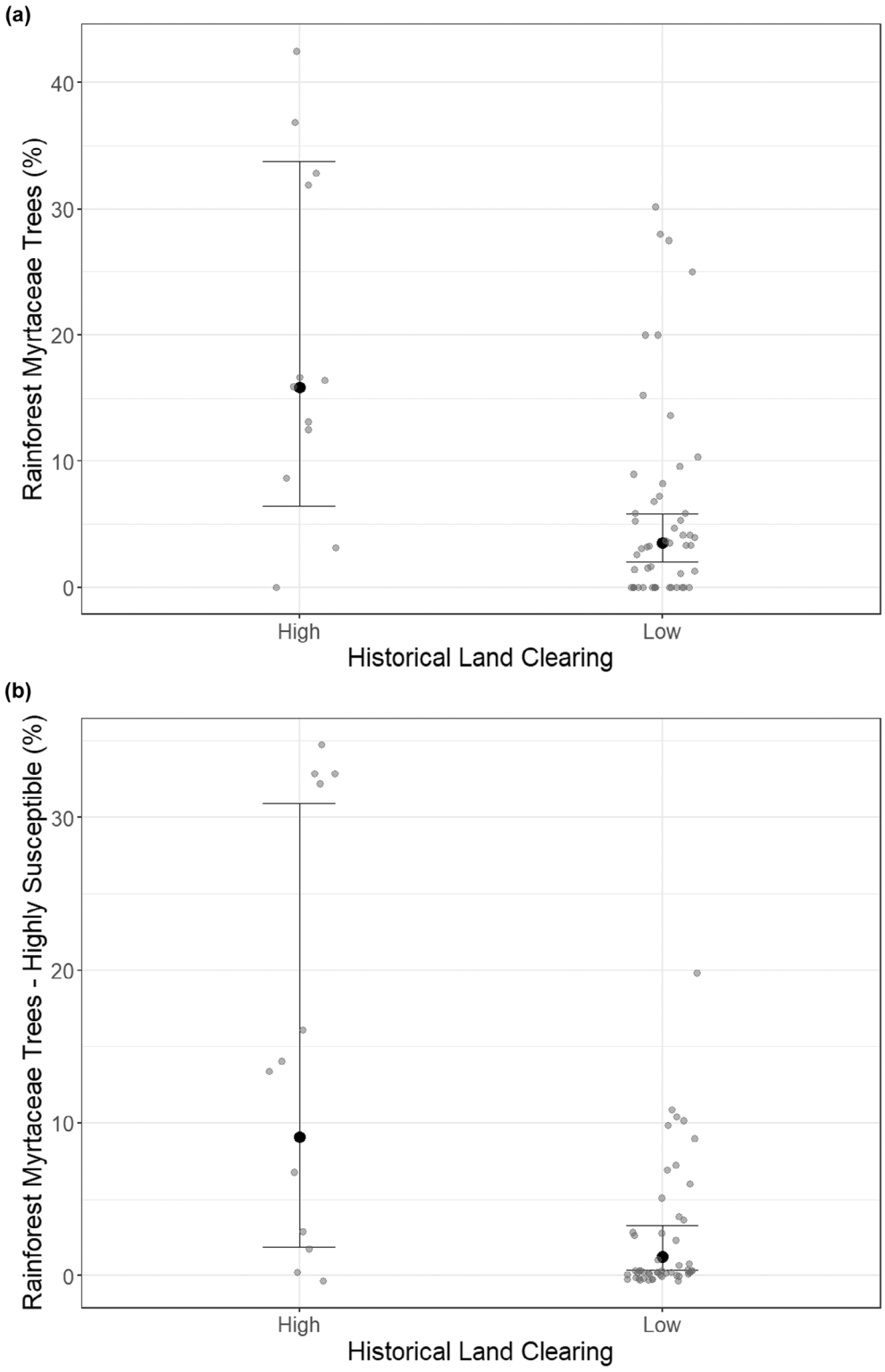


FIGURE 2 Higher proportions of rainforest Myrtaceae trees were recorded at sites that had experienced high historical land clearing, when (a) all rainforest Myrtaceae species were considered and (b) only highly susceptible species were considered. Error bars represent 95% credible intervals. Grey points represent surveyed transects and black points represent median values.

were considered (median = 2.10, 95% CI = 0.43–4.10; Figure 2b), but not when only low susceptibility species were considered (median = 0.17, 95% CI = −1.27 to 1.65). However, the CI, representing the range within which the model predicts with 95% probability that the true estimate lies (McCarthy, 2007; pg. 28–29), was wide indicating some uncertainty around the magnitude of the effect.

At total of 285 rainforest Myrtaceae trees from 11 species were recorded across the 21 sites. The representation of trees from

species categorised as having low or high susceptibility trees was relatively balanced at 48% and 52%. *Archirhodomyrtus beckleri* was the most recorded species, representing 41% of the total rainforest Myrtaceae trees and 77% of the highly susceptible trees (Supporting Information S4). The distribution of this species across sites was spatially clumped, with 83% recorded at three of the four high historical land clearing sites. All other rainforest Myrtaceae species had less than 50% of trees at these sites (Supporting Information S3). This suggests that the positive effect of historical land clearing on the proportion of rainforest Myrtaceae was largely being driven by this single species.

There was a positive effect of historical land clearing on disease score (median = 1.57, 95% CI = 0.74–2.43). Sites that had experienced high levels of historical land clearing had higher disease scores with a median of 0.71 (95% CI = 0.54–0.84) or 3.2 (50–90% branch death) on the original scoring scale (Figure 3a). This is compared to a median of 0.34 (95% CI = 0.25–0.43) or 1.5 (between 0%–10% and 10%–50% branch death) on the original scoring scale, at sites with low historical land clearing (Figure 3a). The high posterior probability for a positive effect was maintained when scores from only highly susceptible species were included (median = 1.06, 95% CI = 0.06–2.03; Figure 3b), but not when only scores from low susceptibility species were included (median = −0.25, 95% CI = −0.95 to 0.37). However, the wide CI again indicates some uncertainty around the magnitude of the effect when only considering highly susceptible species.

There was high posterior probability of a positive correlation between disease score and the proportion of rainforest Myrtaceae trees (all levels of susceptibility) (median = 5.50, 95% CI = 2.40–8.60; Figure 4a). Evidence for this correlation remained when scores from only highly susceptible rainforest Myrtaceae trees were included (median = 6.08, 95% CI = 2.93–9.36; Figure 4b), but not when scores from only low susceptibility species were included (median = −0.29, 95% CI = −2.62 to 1.89).

There is a strong probability that the effect of forest edge on the proportion of rainforest Myrtaceae trees or disease score is negligible, as indicated by the inclusion of zero in the 95% CIs (median = −0.28, 95% CI = −0.68 to 0.12 and median = −0.22, 95% CI = −0.77 to 0.34).

4 | DISCUSSION

Global trade and tourism continues to facilitate the movement of plant pathogens into habitats outside of their native range (Ghelardini et al., 2016). Research that investigates the density and distribution of susceptible species and how this affects disease impacts is key to informing targeted management of affected forest patches. In this study, the density of susceptible rainforest Myrtaceae trees was associated with historical land clearing, but not with current land tenure. Land use patterns in South-East Queensland and Northern New South Wales have changed substantially over the last 150 years, with the changing nature of the forestry, dairy and banana growing industries and changes in conservation priorities with more private properties being owned for lifestyle in the region studied (Department of Natural Resources, 1999; Elliott, 1977; Horsman, 1995). In this study, forests that have re-established after land clearing were observed across all land tenures. Communication with local landowners and land managers confirmed areas that were previously managed for forestry or farming that are now managed as reserves. This highlights that current management does not always reflect past land use and that past patterns of disturbance can affect the composition of current tree communities (Lunt & Spooner, 2005).

Historical land clearing appeared to favour some susceptible species that can act as early colonisers, likely increasing their density. This was only apparent when highly susceptible species were considered in the analyses and appeared to be largely driven by a single species *Archirhodomyrtus beckleri*. Trees from this species represented close to half of all rainforest Myrtaceae trees recorded, with most of these trees observed at three of the four sites that had experienced high historical land clearing.

Several factors likely interacted to facilitate the abundance of *Archirhodomyrtus beckleri* at sites that had experienced high historical land clearing. This species was one of few early coloniser species listed as dominant or frequent in multiple canopy layers of this forest community (Queensland State Government, 2021). It is associated with poorer soils (Floyd, 2008), corresponding with the metasediment parent material underlying this forest community (Queensland State Government, 2021). Its fruits contain a high abundance of seeds (Cooper & Cooper, 2013), likely aiding dispersal and recruitment. *Archirhodomyrtus beckleri* also has the capacity to resprout from basal buds (Benwell, 2024). It is possible that repeated clearing also enhanced its abundance at our study sites, as has been evidenced for other rainforest Myrtaceae species (Floyd, 1990).

The inclusion of sites with different land clearing histories was incidental as our initial design was based on land tenure. This resulted in an imbalance of sites across the two levels (high clearing: $n = 4$ compared to low clearing: $n = 17$) and represents a limitation in our study. Low sample size can result in weaker precision around model estimates (Harrison, 2015). This appears to have been the case in our study with consistently wider 95% CIs associated with the high historical land clearing sites compared to the low historical land clearing sites. While our models indicate a high probability of a positive effect of historical land clearing, the strength of the effect is less certain.

Differences in past land use and forest recovery existed between the high historical land clearing sites. While three of these sites were largely open in the 1960s and appear to have regenerated naturally, one site was under a banana plantation and forest regeneration was actively assisted by the landowners through actions such as weed removal. We did not record *Archirhodomyrtus beckleri* in our surveys at the latter site, and the proportions of rainforest Myrtaceae trees recorded were comparable with those at low historical land clearing sites. This suggests that there were differences in plant community assembly between these sites. Future studies should investigate this further to better understand how different land use legacies may affect the density of susceptible species.

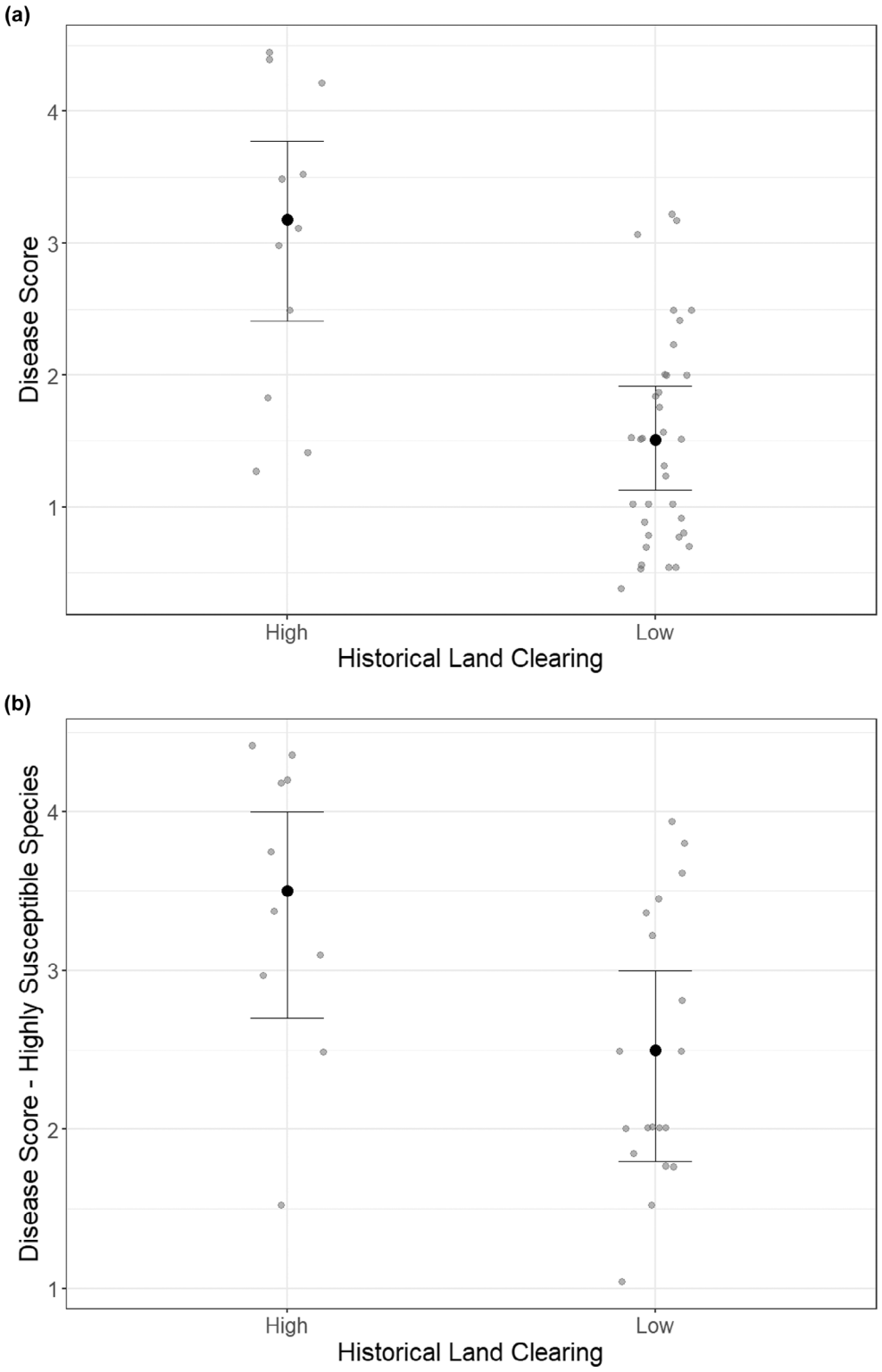


FIGURE 3 Higher disease scores were recorded at sites that had experienced high historical land clearing, when (a) scores from all species were considered and when (b) only highly susceptible species were included. Disease scores have been back transformed to the original scale (0–4.5). Error bars represent 95% credible intervals. Grey points represent surveyed transects and black points represent median values.

Disturbance history has also been correlated with changes in the representation of susceptible tree species in other studies. In the southwest of the United States, low fire frequency was associated with higher abundances of *Umbellularia californica* trees (Meentemeyer et al., 2008; Simler-Williamson et al., 2021). A species that is susceptible to the pathogen *Phytophthora ramorum* and its high

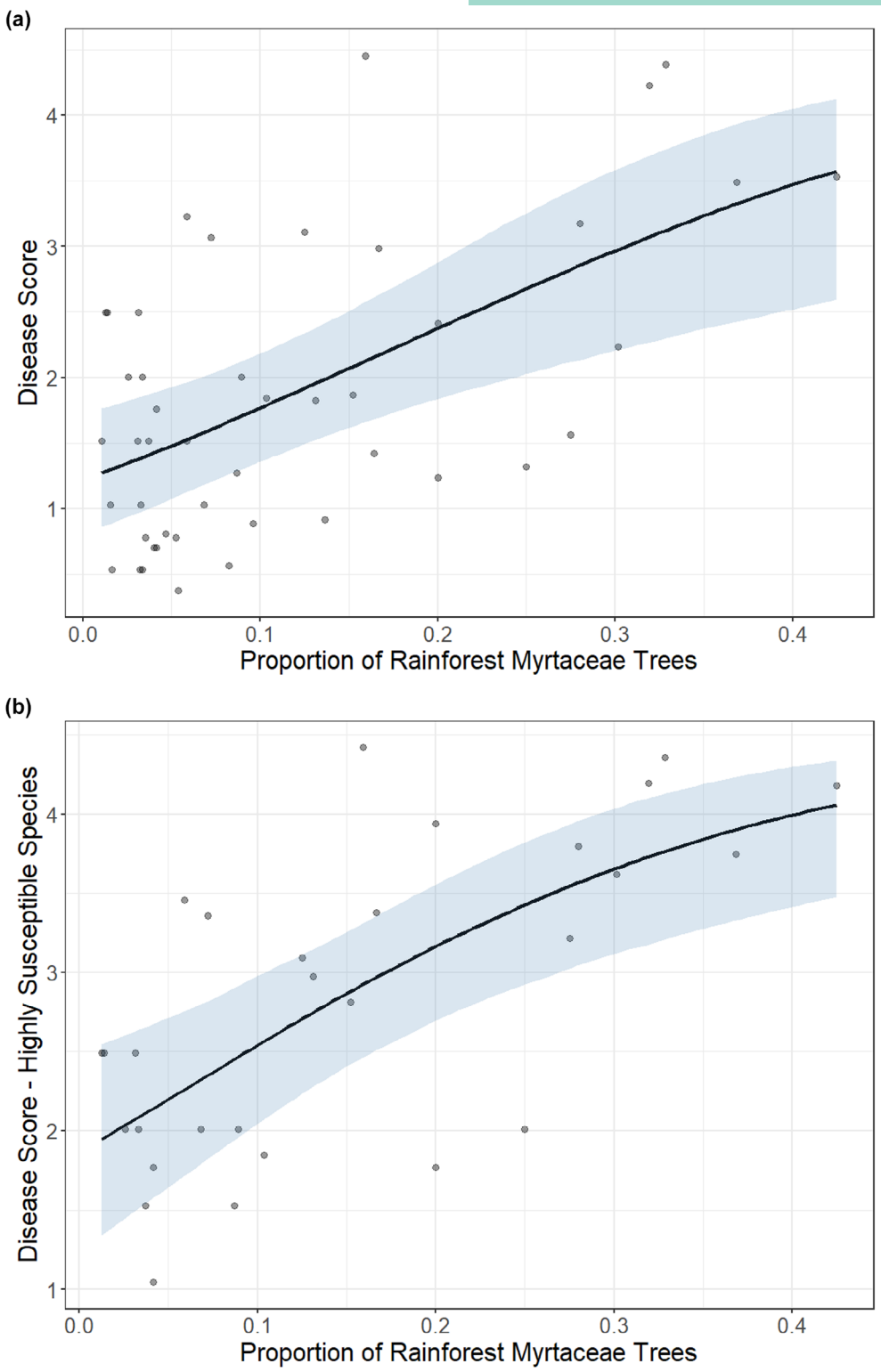


FIGURE 4 A positive correlation between disease score and the proportion of rainforest Myrtaceae trees (all levels of susceptibility) was observed, when (a) scores of all species were included and when (b) scores from only highly susceptible species were included. Points represent surveyed transects. Disease scores have been back transformed to the original scale (0–4.5). Blue shading represents 95% credible intervals.

plant density and high inoculum load are suggested to be a key driver of disease in these forests (Dillon & Meentemeyer, 2019). In the northeast of the United States, fire was suggested to reduce disease impacts of the plant pathogen *Discula destructiva* via changes in the composition of the overstorey forest canopy layer (Holzmueller et al., 2008). Fire was suggested to favour early successional species

and the opening up of the canopy creating environmental conditions less favourable for the disease (Holzmueller et al., 2008). Therefore, some forest successional stages may be more susceptible to pathogen impacts than others based on the relative abundance of key plant host species.

Sites that had experienced higher levels of land clearing were also associated with higher disease scores. Increased inoculum loads in other forests affected by non-native plant pathogens, including *Phytophthora ramorum* and *Hymenoscyphus fraxineus*, have been associated with the density of susceptible and competent trees (Dillon & Meentemeyer, 2019; Martin et al., 2025). Increased inoculum levels have been correlated with increased severity of myrtle rust impacts under laboratory conditions (Ireland & Pegg, 2020). In our study, the abundance of *Archirhodomyrtus beckleri* trees was quite high at some sites, particularly at one of the high historical land clearing sites, where it was estimated at 2033 ± 328 per ha. While most of these trees are now surviving as basal re-sprouts or are exhibiting high branch death, it is likely that in the years when myrtle rust first arrived and these trees had largely intact canopies with a high abundance of susceptible foliage, it also reflected elevated inoculum loads. This high susceptible plant density may have resulted in higher disease incidence and severity of impact.

Interrupted spore transmission is another mechanism that may have contributed to the positive association between the relative abundance of susceptible trees and mean disease score. An increased abundance of non-susceptible species in a patch can increase the probability that these trees will disrupt the transmission of spores, reducing the chance that they will reach and infect a susceptible host (Keesing et al., 2006). The spores of myrtle rust are predominantly wind dispersed (Pegg et al., 2014). It is possible that forest patches with lower proportions of susceptible trees may have had reduced spore transmission between susceptible trees. This, in turn, may have facilitated the lower levels of branch death observed.

The level of susceptibility of species to myrtle rust affected patterns of disease score. When only species with a low susceptibility to myrtle rust were considered in the analyses, no evidence for a difference in disease score between sites with different levels of historical land clearing was observed nor was there evidence for a correlation between disease score and the proportion of rainforest Myrtaceae. We recorded six species that were categorised as low susceptibility. Our categories were based on ratings of susceptibility collated in Makinson (2018) that were developed from observations of infection on susceptible foliage and dieback due to myrtle rust. The mean and median disease score for trees from species categorised as low susceptibility was 1, representing 0%–10% branch death, and was consistent across sites of both high and low historical land clearing.

Low susceptibility species, particularly *Pilidiostigma glabrum* and *Syzygium oleosum*, were not distinctly aggregated but tended to be recorded at low abundance at most sites (Supporting Information S4). Species of low susceptibility and competence have been observed to have limited influence on disease dynamics in forests affected by *Phytophthora ramorum* in the United States (Rosenthal et al., 2021). Our results indicate that low susceptibility species may be less important in determining myrtle rust impacts in this forest community.

We predicted that forest edges may be more prone to myrtle rust impacts; however, there was not enough edge contrast at many of our sites to detect an effect. Many of the edges we used were not associated with open canopy but rather enclosed within a forest patch (e.g. walking tracks or forestry roads), likely reflecting little change in environmental conditions such as relative humidity or canopy cover. Increases in these two factors with distance from a forest edge were suggested to correlate with more severe myrtle rust impacts on *Lophomyrtus bullata* Burret trees in New Zealand (McCarthy et al., 2025). Susceptible trees recorded along these more enclosed edges would also likely experience substantially different exposure to wind-borne spores of myrtle rust in comparison to more exposed edges along pastures or main roads.

Differences in ongoing disturbance regimes between edge types also likely influenced patterns in the recruitment of susceptible early coloniser species. For example, the maintenance of vegetation along paved roads likely represents a larger disturbance than maintenance of vegetation along a walking track. However, low replication among these edge types prevented us from testing these hypotheses.

Land clearing history could be a useful tool in identifying patches of this wet sclerophyll forest that may be more prone to myrtle rust impacts. Our results suggest that historical aerial imagery could be used to identify forest patches where susceptible species may be more dominant, and therefore at higher risk of more severe impacts from myrtle rust. Once identified, targeted restoration actions could be applied to reduce potential flow on effects of myrtle rust. Actions such as monitoring for weed invasion or reducing the abundance of dead standing trees, flow on effects already identified in some forest patches heavily affected by the pathogen (Pegg et al., 2017; Stevenson, 2023). Further research on varying densities and spatial arrangements of susceptible trees in forest patches and myrtle rust impact would be valuable to inform any re-introduction programmes for susceptible species.

Forest patches with a lower density of rainforest Myrtaceae trees, that is, those exposed to lower levels of historical disturbance, may be valuable targets for plant conservation efforts. These patches may be more likely to contain healthier trees that could be good candidates for germplasm collection for ex situ conservation. Efforts are ongoing to collect cuttings from populations of several myrtle rust affected species, including *Rhodomyrtus psidioides* and *Rhodamnia rubescens*, aiming to capture remaining genetic diversity that can be used for plant breeding programmes (Chen et al., 2025).

Trees in patches that have experienced low historical land clearing may also be good candidates for in situ conservation. Researchers in New Zealand utilised climate and environmental factors to identify possible refugia in the landscape for myrtle rust affected species (Herbert et al., 2025). If similar work was to be undertaken in Australia, land use history could be integrated to help identify priority sites. Targeted management actions such as the application of fungicides could be employed to maintain some ecologically functioning trees in situ. This approach has been beneficial in other

systems; for example, the application of phosphite helped to sustain living populations of 17 susceptible species in a forest community in Western Australia affected by the plant pathogen *Phytophthora cinnamomi* (Barrett & Rathbone, 2018).

This study provides valuable data on impacts of myrtle rust at the plant community level but leaves further questions. *Archirhodomyrtus beckleri* is only one of several rainforest Myrtaceae that is highly susceptible to myrtle rust and can act as early coloniser. Other species include *Rhodamnia rubescens* and *Rhodomyrtus psidioides* (Benwell, 2024; Makinson, 2018). Although *Rhodamnia rubescens* is also characteristic of our wet sclerophyll forest community, a similar association between the density of this species and historical land clearing was not observed. Future research should investigate other types of disturbance (e.g. historical fire regimes or storm events) that could be correlated with the density and distribution of these species. These data would be valuable in identifying possible locations of remnant populations of these species.

5 | CONCLUSIONS

Land use history is variable at the landscape scale. Our results suggest that understanding how land clearing history varies between forest patches can aid in predicting susceptible plant distribution, density and associated myrtle rust disease impacts across the landscape. Maps of past land use could be used to predict the density of susceptible species and the level of branch death by myrtle rust. Forest patches that have experienced low historical land clearing could be surveyed for susceptible trees that remain healthy and be useful for conservation efforts. Forest patches that have experienced high historical land clearing might be more prone to the flow-on effects of myrtle rust, such as the invasion of weeds, and would benefit from ongoing monitoring and restoration interventions. This research contributes to a growing number of studies that have focused on interactions between non-native plant pathogens and other disturbance types (Simler-Williamson et al., 2021). As plant pathogens continue to establish and spread into habitats outside of their native range, research focusing on processes that drive the abundance and distribution of susceptible species will become increasingly valuable globally to inform effective management strategies.

AUTHOR CONTRIBUTIONS

Jennifer Firn and Geoff Pegg acquired the funding; Kristy Stevenson and Jarrod Carlson collected the data; Kristy Stevenson analysed the data; Kristy Stevenson, Jennifer Firn, William McDonald, Jarrod Carlson, Geoff Pegg and Jarrah Wills all contributed to shaping the methods and interpreting the results; Kristy Stevenson led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data associated with this study are open access via the Queensland University of Technology's Research Data Repository (Stevenson & Firn, 2026; https://doi.org/10.25912/RDF_1770334888304).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Rainforest Myrtaceae species observed in our surveys, the susceptibility category used for each species in this paper, and the susceptibility ratings described in Makinson (2018) from which our categories were developed.

Supporting Information S2. Examples of (a) damage consistent with myrtle rust (*Austropuccinia psidii*) on leaves of *Rhodamnia maideniana*. (b) Damage attributed to other pathogens or insects on leaves of *Syzygium oleosum*, *Pilidiostigma glabrum* and *Acmena smithii*.

Supporting Information S3. Species area curves created using data for all tree species ($n = 143$) at the transect level ($n = 63$), calculated using (a) random (final slope = 0.50) and (b) rarefaction (final slope = 0.35) methods from the specaccum() function in the vegan package (Oksanen et al., 2020).

Supporting Information S4. Table listing the rainforest Myrtaceae species observed in our surveys, the representation of each species out of the total rainforest Myrtaceae trees recorded, the percentage of trees from each species that was recorded at high historical land clearing sites, and the number of sites where at least one individual the species was recorded.

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