



## Evolutionary history shapes the susceptibility of an island tree flora to an exotic pathogen



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### ABSTRACT

With globalisation, the world's native biotas are increasingly exposed to disease, parasitism, herbivory and competition from exotic organisms. The vulnerability of native biota to these exotic invasions is exacerbated by human disturbance and global climate change. Rust pathogens are some of the most important plant pathogens, including *Puccinia psidii* (myrtle rust or guava rust) that is now spreading worldwide at an alarming rate. *P. psidii* is native to South America and affects species in the family Myrtaceae, including the economically and ecologically important eucalypts. The Australian continent has a rich myrtaceous flora and is the centre of origin of most eucalypt species. *P. psidii* was first detected in Australia in 2010 and has since rapidly spread along its east coast. We assess the risk this exotic pathogen poses to the eucalypt flora of the southern Australian island of Tasmania, where the first incursion of *P. psidii* was detected in early 2015. Specifically, we tested the relative importance of phylogenetic history, habitat, endemism, and range size in predicting host susceptibility.

Rust screening of seedlings from one to four populations of each of the 30 eucalypt species which are native to Tasmania, revealed significant genetic-based variation in response among host species and populations within the species. Significant population differences in susceptibility were detected in threatened, rare and endemic eucalypt species, as well as Australia's main plantation eucalypt (*Eucalyptus globulus*) and the world's tallest angiosperm species (*Eucalyptus regnans*). A significant proportion of the variation in host species susceptibility to this exotic pathogen was explained by phylogenetic history, while factors such as habitat, endemism and range size had no detectable effect. Species from subgenus *Eucalyptus* (13 species) were more susceptible than those from subgenus *Symphyomyrtus* (17 species) due to differences between the subgenera in the proportion of plants showing a symptomless response. These subgenera are here shown to differ in their leaf oil and wax chemistry. The potential contribution of these differences and other possible mechanisms causing these subgeneric differences in susceptibility are discussed. This study demonstrates the power of a phylogenetic approach to risk assessment for biosecurity and highlights the need for broader resistance screening within and between populations of species of high conservation or economic value.

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### 1. Introduction

With globalisation increasing human-aided dispersal of organisms, the world's native biotas are increasingly exposed to disease, parasitism, herbivory or competition from exotic organisms (Paine et al., 2011; Pearse et al., 2013; Ennos, 2015). This is further exacerbated by human disturbance and global climate change

contributing to the vulnerability of native biota to invasion (Sharan et al., 2010; Alfaro et al., 2014), which in extreme cases may result in widespread community and ecosystem transformation (Bailey et al., 2001). The role of evolutionary history in shaping the outcomes of such biotic invasions is increasingly recognised from multiple perspectives (Gilbert et al., 2012, 2015; Pearse et al., 2013). In the case of invading plants, phylogenetic proximity to the native species may affect their invasive potential (Strauss et al., 2006) and susceptibility to native herbivores (Hill and Kotanen, 2010; Parker et al., 2012). On the other hand, susceptibility of a native

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flora to exotic herbivores and pathogens can depend upon the phylogenetic distance between the native species and co-evolved host (Gilbert et al., 2012; Ennos, 2015). Such predictability is important to understand as it allows management actions to be prioritised when biodiverse floras are at risk (Thrall et al., 2011; Gilbert et al., 2012, 2015).

Globally, islands are hotspots of biodiversity (Bisconti et al., 2013), with levels of species richness dependent upon factors such as area, level of isolation, elevation range and climatic similarity with surrounding land mass (Keitt et al., 2011; Weigelt and Krefl, 2013). They generally have greater levels of endemism relative to comparable mainland regions (Keitt et al., 2011), but are often more vulnerable to invasion (Lonsdale, 1999; Caujape-Castells et al., 2010). While comprising only  $\approx 5\%$  of the earth's surface, islands have experienced 64% of IUCN-listed extinctions and have 45% of IUCN-listed critically endangered species (Keitt et al., 2011). Island biota are thus a focus of conservation concern, with pathogen introduction listed as one of the many threatening processes (Heywood, 2011).

Rust pathogens are some of the most important plant pathogens worldwide. *Puccinia psidii* (Pucciniales, Pucciniomycotina) affects species in the family Myrtaceae, producing spore filled lesions on young actively growing leaves, shoots, flower buds and fruits; which can result in death of highly susceptible plants (Coutinho et al., 1998; Carnegie et al., 2010). Before reaching Australia, the known host range of *P. psidii* was 129 species from 33 genera worldwide (Carnegie and Lidbetter, 2012), with significant impacts on plant industries such as guava (*Psidium guajava*), all spice (*Pimenta dioica*), and eucalypts (MacLachlan, 1938; Ferreira, 1983; Ferrari et al., 1997; Grattapaglia et al., 2012). *P. psidii* has long been recognised as a serious quarantine threat to many countries, outside of its native South America, due to this unusually broad host range (Coutinho et al., 1998; Park et al., 2000; Glen et al., 2007). Australia was flagged as a country particularly at risk because much of its flora is dominated by myrtaceous species, including the eucalypts (Glen et al., 2007). Since the first report of the disease on guava in Brazil, it has been reported throughout Central and South America, and Florida on mainland USA (Coutinho et al., 1998). In 2005 the pathogen was detected outside of the America's for the first time, in Hawaii, and is spreading with increasing rapidity, having now been found in Australia, China, Indonesia, Japan, New Caledonia, and South Africa (Uchida et al., 2006; Kawanishi et al., 2009; Zhuang and Wei, 2011; Giblin and Carnegie, 2014; Roux et al., 2013; McTaggart et al., 2016).

The first report of *P. psidii* in Australia was in the south-east (the central coast of N.S.W.) in April 2010 (Carnegie et al., 2010). It spread rapidly and was reported well northward in Queensland by December 2010 and southward in Victoria by December 2011. This spread exposed many naïve hosts to the pathogen, increasing the known host range to 232 species from natural infections in Australia, and over 450 species globally (Giblin and Carnegie, 2014; Pegg et al., 2014b; Carnegie et al., 2016). While *P. psidii* is often referred to as 'eucalypt rust' or 'guava rust', only a single variant currently occurs in Australia and its common name is 'myrtle rust' (Carnegie and Lidbetter, 2012; Machado et al., 2015; Sandhu et al., 2016). By early 2015 *P. psidii* was found in several nurseries and gardens on the southern temperate island of Tasmania, which is separated from mainland Australia by the 240 km wide Bass Strait (Fig. 1). While climatic models suggest that only a small area in the north of the island is climatically suited for persistent populations of *P. psidii*, most areas are suitable for some population growth and under a warming climate the area of suitability is expected to increase (Kriticos et al., 2013).

The rugged island of Tasmania is home to 30 native *Eucalyptus* species which have a well-studied evolutionary history (McKinnon et al., 2004; Harrison et al., 2014). They occupy diverse habitats

from sea-level to the high-altitude tree-line (Williams and Potts, 1996) and range in habit from a small alpine shrub (*Eucalyptus vernicosa* – McGowen et al., 2001) to giant forest trees, including the world's tallest angiosperm (*Eucalyptus regnans* – Grattapaglia et al., 2012). The island includes one of the 14 centres of endemism identified for eucalypts (Gonzalez-Orozco et al., 2014). Sixty percent of the species are endemic to Tasmania, with two endemic taxa – *Eucalyptus morrisbyi* and *Eucalyptus gunnii* subspecies *divaricata* – threatened and in decline (Jones et al., 2005; Sanger et al., 2011). Many of the wet sclerophyll species such as *Eucalyptus obliqua*, *Eucalyptus delegatensis* and *E. regnans* are economically important for forestry (Baker and Read, 2011). In addition, the island is the centre-of-origin of several species under domestication – the frost resistant *E. gunnii* in France (Potts and Potts, 1986) and the Tasmanian blue gum, *Eucalyptus globulus*, which is the main plantation eucalypt grown in pulpwood plantations in temperate regions of the world (Doughty, 2000).

In view of the risk posed by *P. psidii* and the high biological and economic importance of the island's eucalypt flora, we undertook a screening of seedlings of all species to help prioritise response actions. The eucalypts of the island belong to two subgenera – subgenus *Symphyomyrtus* (17 species) and subgenus *Eucalyptus* (13 species; [previously informal subgenus *Monocalyptus*]). We thus specifically tested whether evolutionary history, reflected by common subgenus, was more important than other factors such as habitat, endemism or range size in predicting the susceptibility of this naïve, tree flora to an introduced pathogen.

## 2. Materials and methods

### 2.1. Sampling of the island's eucalypts

Between one and four populations of each of the 30 eucalypt species native to the island of Tasmania were sampled, giving a total of 85 populations (Fig. 1). Seed was sampled from across the geographic range of each species, subject to availability. Populations were represented by bulks of open-pollinated seed collected from between 3 and 50 trees growing in natural forests, with over 1100 native trees represented. The only non-wild exception was one population of the endangered *E. morrisbyi* (mor2) which, as seed is scarce in the wild, was derived from open-pollinated seed collected from 10 unrelated trees in a seed orchard. Full population details including, latitude, longitude, altitude, seed provider and the number of trees sampled, are given in Supplementary Material Table S1.

### 2.2. Seedling growth

Seedlots were stratified in moist vermiculite at 4 °C for between two and six weeks (depending upon known requirements for each species) and then dispatched to the Plant Breeding Institute (PBI), University of Sydney for germination and growth. For germination, seedlots were spread on the soil (coarse sand soil mix) surface of individual 25 cm-diameter pots that were randomised in a greenhouse. When seedlings began to emerge they were pricked out into individual 9 cm-diameter pots filled with a mixture of fine bark and coarse sand. Seedlings were initially grown in population plots that were randomised in position within the greenhouse while seedlings became established and then re-arranged in a randomised block design comprising 30 replicate blocks, with each population generally represented once per replicate. Where insufficient seedlings for a population were available, these were randomly allocated to replicate blocks and vacant treatment positions filled with either another under-represented population or fillers from another population with excess seedlings. Replicate blocks were sequentially screened for *P. psidii* susceptibility in

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