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The Enemy of My Enemy? Emergence of the rust pathogen Austropuccinia psidii is associated with the rapid decline of the invasive tree Syzygium jambos in the Galápagos Islands

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Dear Editor,

We are pleased to submit our Original Paper entitled “The enemy of my enemy? Emergence of the rust pathogen *Austropuccinia psidii* is associated with the rapid decline of the invasive tree *Syzygium jambos* in the Galápagos Islands” for consideration for publication in Biological Invasions.

In this study, we document morphological and molecular identification of *Austropuccinia psidii* infecting invasive *Syzygium jambos* on San Cristóbal Island, Galápagos, together with an approximately 73% reduction in the invasive host’s forest cover between 2018 and 2024. By integrating remote sensing and field observations with pathogen identification, our study highlights an ecological paradox in which an invasive pathogen may contribute to the decline of an invasive tree while potentially posing risks to native and endemic Myrtaceae. These findings provide insight into interactions among introduced species and their implications for invasion dynamics and biodiversity conservation in island ecosystems.

This manuscript represents original work that has not been published previously and is not under consideration for publication elsewhere. All authors have read and approved the final version of the manuscript, agree with its submission to Biological Invasions, and have made substantial contributions to the study.

Thank you for your consideration. We appreciate your time and look forward to your response.

Sincerely,

Gonzalo Rivas-Torres

on behalf of all authors

We are waiting for your comments and revision of this manuscript,

Best Regards,

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The enemy of my enemy? Emergence of the rust pathogen *Austropuccinia psidii* is associated with the rapid decline of the invasive tree *Syzygium jambos* in the Galápagos Islands

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Abstract

The introduction of invasive plant species has become a major threat to the unique biodiversity and ecological integrity of the Galápagos Islands. One of the most aggressive invaders is *Syzygium jambos* (Myrtaceae), which forms dense tree stands that suppress native vegetation and alter ecosystem functioning. Remarkably, populations of this invasive rose apple tree have undergone a pronounced decline on San Cristóbal Island in recent years. In this study, we combined remote sensing with pathogen identification to investigate this phenomenon. Spectral and spatial analyses revealed an approximate 73% reduction in *S. jambos* tree cover between 2018 and 2024. Concurrently, symptomatic leaves were examined using morphological characterization and molecular diagnostics. Nested PCR amplification followed by internal transcribed spacer (ITS) region sequencing confirmed the presence of *Austropuccinia psidii*, a myrtle rust fungus known to infect members of the Myrtaceae family, in symptomatic *S. jambos* leaves. This study combines morphological and molecular identification of *A. psidii* infecting *S. jambos* in the Galápagos Islands with a landscape-scale assessment of the invasive host's decline. Our findings document an ecological paradox in which an invasive fungal pathogen infects an invasive tree, potentially contributing to its decline while posing a risk to native and endemic Myrtaceae. This interaction highlights how associations among non-native species may influence invasion dynamics, with potentially contrasting consequences for biodiversity conservation in vulnerable island ecosystems.

Keywords: Galápagos, *Syzygium jambos*, rose apple, *Austropuccinia psidii*, myrtle rust, invasive species

Introduction

The Galápagos Islands are globally renowned for their exceptional biodiversity and remarkable levels of endemism, making them one of the world's most important laboratories for ecology and evolution (UNESCO World Heritage Centre n.d). Of the nearly 500 native plant species recorded in the archipelago, more than 30% are endemic (Tye et al. 2002). To protect this unique biodiversity, 97% of the archipelago was designated as Galápagos National Park in 1959 and later recognized as a UNESCO World Heritage Site in 1978 (Walsh et al. 2008). Despite these conservation efforts, increasing tourism, trade, and human settlement have greatly accelerated the introduction of non-native species to the archipelago (PNG 2014; Walsh et al. 2008).

Introduced species represent one of the greatest threats to the terrestrial ecosystems of the Galápagos Islands (Tye et al. 2001). Once established, invasive plants can outcompete native vegetation, alter ecosystem processes, modify soil properties, and reduce biodiversity, ultimately threatening the persistence of endemic species (Mooney and Hobbs 2000; Walther et al. 2009). Consequently, understanding the factors that determine the spread, persistence, and eventual decline of invasive species has become a major priority for biodiversity conservation in island ecosystems (Loope et al. 1988).

The Charles Darwin Foundation's Introduced Species Dashboard currently records 1,644 introduced taxa in the Galápagos, including subspecies, plant varieties, and cultivars, of which 1,577 are established in the archipelago (Charles Darwin Foundation n.d.).

Beyond their individual impacts, the increasing accumulation of introduced species in the Galápagos may also facilitate novel ecological interactions among non-native organisms. Such interactions, including those between introduced plants and pathogens, could generate unexpected consequences for invasion dynamics and native biodiversity (Parker and Gilbert 2004), yet remain poorly understood in island ecosystems (Muñoz-Gallego et al. 2025).

One of the most problematic invasive plant species in the Galápagos is *Syzygium jambos* (rose apple), a tree native to Southeast Asia that was introduced to Floreana Island in the late 1920s and to San Cristóbal around 1950 (Lundh 2006). Since its introduction, rose apple has spread extensively across several Galápagos islands, including Floreana, San Cristóbal, Isabela, and Santa Cruz, where it forms dense monospecific stands that suppress native vegetation by reducing light availability, competing for resources, and altering soil properties (Rentería Bustamante et al. 2007). Similar concerns regarding the impacts and management of invasive plants in the archipelago have been reported for other highly invasive species,

such as *Rubus niveus* (Barriga-Medina et al. 2025). Recent land-cover analyses estimated that San Cristóbal harbors the largest population of rose apple trees in the archipelago, covering approximately 384 ha. Most infestations occur in the humid highlands of the east-central region of this island surrounding El Progreso (Figure 1) (Laso et al. 2019).

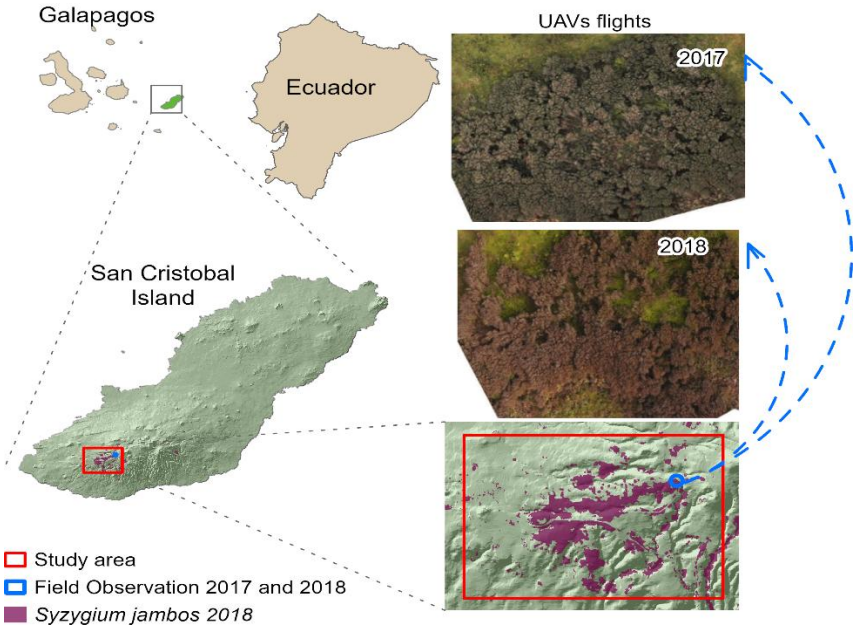


Fig. 1 Location of the study area on San Cristóbal Island, Galápagos, showing the spatial distribution of *Syzygium jambos* in 2018. Insets illustrate UAV-based imagery of representative *S. jambos* field observations from 2017 and 2018 (Information based on Laso et al. 2019)

The remarkable success of many invasive plant species has often been explained by the Enemy Release Hypothesis, which proposes that introduced species escape the specialist herbivores and pathogens that regulate their populations in their native range (Keane and Crawley 2002). Over time, however, invasive species may accumulate novel herbivores and pathogens in their introduced range, reducing their competitive advantage and altering invasion dynamics. Such pathogen-mediated declines may represent an important natural mechanism regulating invasive plant populations (Flory and Clay 2013). These processes are particularly relevant in island ecosystems, which are highly vulnerable to biological invasions due to their geographic isolation, high levels of endemism, and ecological specialization (Muñoz-Gallego et al. 2025). The introduction of exotic species into these fragile ecosystems creates opportunities for novel host-pathogen interactions that did not exist within the native ranges of the interacting species (Parker and Gilbert 2004). In some cases, invasive plants may become infected by newly acquired pathogens that inadvertently act as natural biological control agents, slowing their spread or contributing to population decline (Mitchell and Power 2003; Flory et al. 2011). At the same time, the emergence of such pathogens also poses ecological risks, as they may spill over to native species or amplify disease pressure through spillback, potentially threatening endemic biodiversity (Strauss et al. 2012). Understanding these novel ecological interactions is therefore essential for predicting both the ecological consequences of biological invasions and the opportunities and risks associated with the natural regulation of invasive species.

Evidence that this process is occurring in the Galápagos comes from our finding that the invasive rust fungus *Austropuccinia psidii* is infecting the invasive tree *S. jambos* in the archipelago. Rose apple is highly susceptible to a range of fungal pathogens, including leaf spot diseases, anthracnose, root rot, and, most notably, myrtle rust caused by *A. psidii* (syn. *Puccinia psidii* G. Winter), which can induce severe defoliation, flower and fruit loss, dieback, and ultimately reduce tree fitness (Tessmann et al. 2001; Beenken 2017). Commonly known as myrtle rust, allspice rust, or guava rust, *A. psidii* was first reported as a pathogen of allspice in 1930 and has since emerged as one of the most destructive pathogens of Myrtaceae in tropical and subtropical regions (Uchida and Loope 2009). Remarkably, following its introduction into new regions, *A. psidii* has repeatedly been detected first on *S. jambos,* including in Puerto Rico, where outbreaks began in 2006 (Burman et al. 2017), and in Hawaii, where it was first reported in 2005 on young

rose apple leaves (Killgore and Heu 2007). Its occurrence on *S. jambos* in the Galápagos suggests that not only invasive plants, but also their associated pathogens, are becoming established in the archipelago. Whether *A. psidii* ultimately contributes to the natural suppression of *S. jambos* populations, or instead poses an additional threat through spillover to native and endemic Myrtaceae, remains unknown. Understanding the emergence and ecological consequences of such novel interactions is therefore critical for predicting invasion dynamics and informing conservation strategies in island ecosystems.

Therefore, in this study, we combine pathogen identification with spectral and spatial analyses of the invasive host's decline on San Cristóbal Island to examine the ecological implications of this interaction between two introduced species. Specifically, we (i) characterize the spectral and spatial distribution of *S. jambos* trees on San Cristóbal Island, (ii) document and sample the rust disease, (iii) identify the pathogen using morphological and molecular approaches, and (iv) discuss the ecological significance of this emerging interaction and its implications for the management of invasive species and the conservation of Galápagos biodiversity.

Materials and Methods

Spectral and spatial analysis of *Syzygium jambos* on San Cristóbal Island

To assess temporal changes in the distribution and canopy condition of rose apple on San Cristóbal Island, we conducted an exploratory analysis using multispectral satellite imagery. Temporal changes in canopy spectral profiles were examined using imagery from NASA's Landsat satellite mission (30-m spatial resolution), which provides long-term multispectral observations in the visible, near-infrared (NIR), and shortwave infrared (SWIR) regions of the electromagnetic spectrum. These spectral regions are widely used to assess vegetation condition because NIR reflectance is primarily related to leaf structure and biomass, whereas SWIR is sensitive to vegetation water content and physiological stress (Tucker 1979; Gao 1996; Asner 1998; Ji et al. 2011; Li et al. 2014; Kim et al. 2015).

Landsat imagery from 2000 onwards was screened for suitability. Owing to the persistent cloud cover over the Galápagos Islands, only scenes with sufficient visibility over the study area were retained. After reviewing the complete Landsat archive, suitable imagery was available for only seven years (Table S1), all acquired during the wet season (January-May), when cloud cover is generally lowest. Data from the Landsat 7 Enhanced Thematic Mapper Plus (ETM+) and Landsat 8 Operational Land Imager (OLI) sensors were used.

Vegetation changes were assessed by generating false-color composites (RGB: NIR-SWIR-Red), which facilitate visual interpretation of canopy condition through changes in spectral response. In addition, reflectance values were extracted from a fixed location within a dense patch of *S. jambos* forest to compare spectral signatures among years and identify temporal shifts associated with the canopy decline.

To quantify spatial changes in *S. jambos* tree cover, we used high-resolution (3-m) multispectral imagery from the PlanetScope constellation (Planet Labs). Based on the availability of cloud-free imagery and unmanned aerial vehicle (UAV) field observations documenting canopy dieback in 2017 and 2018 (Fig. 1), images acquired during the wet season of 2018, 2023, and 2024 were selected for analysis. An unsupervised ISODATA classification was performed to distinguish two land-cover classes: *S. jambos* and non-*S. jambos*. The resulting classifications were used to estimate changes in the spatial extent of *S. jambos* during the study period.

The spectral and spatial analyses conducted in this study were intended as an exploratory assessment rather than a comprehensive remote-sensing study. Their primary purpose was to detect broad patterns of canopy decline and changes in the distribution of *S. jambos*, thereby providing spatial context for the ecological and pathological observations presented in this study.

Macroscopic and microscopic identification of the pathogen

Leaves of rose apple displaying typical rust symptoms were collected in 2021 on San Cristóbal Island, Galápagos (0°54'33.5"S 89°32'13.4"W). Symptoms included chlorotic lesions associated with yellow to orange uredinial pustules on the leaf surface. Samples were transported under refrigerated conditions to the Microbiology Laboratory of the Galapagos Science Center (GSC) for morphological characterization and further processing.

Macroscopic examination was performed using an AmScope LED-144S stereomicroscope to document the distribution, color, and morphology of the rust pustules. For microscopic examination, fungal spores were collected from uredinia using the adhesive tape method (Urzì and De Leò 2001). The tape was mounted directly onto a microscope slide and examined with a Leica DM750 light microscope at 40× and 100× magnification. Spore morphology and other diagnostic structures were photographed and compared with published taxonomic descriptions (Beenken 2017) to enable preliminary identification of the pathogen.

Molecular identification of the pathogen

Molecular identification of the pathogen was performed by extracting DNA from infected *S. jambos* leaf tissue. Because rust fungi are obligate biotrophs and recovering sufficient pathogen DNA from infected plant tissue can be challenging, three different sample preparation methods were evaluated to optimize fungal DNA recovery. A total of four infected samples were processed using these three approaches. First, infected leaves were washed to obtain one suspension enriched in fungal spores. Second, fungal pustules were carefully scraped from the leaf surface and transferred to one sterile Eppendorf tube. Third, two samples of infected leaf tissue, including the associated fungal material, were processed directly. Genomic DNA was extracted from all samples using the Dneasy PowerSoil Kit (Qiagen), following the manufacturer's instructions. DNA extracted from *Fusarium triseptatum* (Llerena-Llerena et al. 2025) was included as a positive amplification control for ITS1F/ITS4 and as a non-target DNA control for the *A. psidii*-specific primer pairs. Nuclease-free water served as the no-template (negative) control.

A conventional PCR was first performed to amplify the fungal internal transcribed spacer (ITS) region of the ribosomal DNA using the universal fungal primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3') (Gardes and Bruns 1993) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) (White et al. 1990). To increase specificity for *A. psidii,* a nested PCR was subsequently performed following Langrell et al. (2008). The first-round (outer) PCR used ITS region primer pair Ppsi1 (5'-TTCTACCTTATTACATGTAGCT-3') and Ppsi6 (5'-GTCATATTGACAGGTTAGAAGC-3'), followed by a second-round (inner) PCR using primers Ppsi2 (5'-ATAGTAATTTGGTATACGTGGC-3') and Ppsi4 (5'-GTCAATCCAAATCAAAGTATG-3'). First-round PCR products were diluted 1:5 and used as template for the nested, second-round amplification. PCR reactions were carried out in a Labnet Multigene thermocycler in a final volume of 25 µL. Cycling conditions consisted of an initial denaturation at 94°C for 3 min, followed by 30 cycles of denaturation at 94°C for 1 min, annealing at 55°C for the ITS1F/ITS4 and Ppsi1/Ppsi6 primer pairs or 57°C for the Ppsi2/Ppsi4 primer pair for 1 min, and extension at 72°C for 1 min, with a final extension at 72°C for 10 min. PCR products were separated on a 2% agarose gel and visualized using a Labnet Enduro GDS gel documentation system (Labnet International). Amplicons yielding the expected fragment size were purified and submitted to Macrogen (Seoul, South Korea) for Sanger sequencing. The resulting sequences were compared against the National Center for Biotechnology Information (NCBI) nucleotide database using the BLASTn tool to determine the closest taxonomic matches.

Results

Landscape-scale spectral changes reveal progressive decline of invasive *Syzygium jambos*

Multitemporal spectral analysis of false-color Landsat composites (RGB: NIR-SWIR-Red) revealed a pronounced temporal change in the spectral characteristics of rose apple forest stands within the San Cristóbal study area (Fig. 2). In the earliest images (2001 and 2009), the forest patches displayed dark red tones, characteristic of healthy, dense vegetation. By 2016, color changes became apparent along the forest edges, with dark red gradually transitioning to dark green, indicating altered vegetation properties. In 2017, most forest patches exhibited predominant dark green tones, suggesting substantial changes in canopy condition, while the overall forest structure remained largely intact.

The spectral changes became more pronounced in subsequent years. By 2019, nearly the entire rose apple stand exhibited blue-green tones, indicative of widespread canopy stress and decline in vegetation health. In 2023, lighter green colors began to dominate the landscape, accompanied by clear signs of forest fragmentation evidenced by green patches. By 2024, most of the affected zone exhibited light green tones that no longer corresponded to those typical of mature rose apple forest, suggesting extensive canopy loss and replacement by herbaceous and shrubby vegetation.

The temporal spectral trajectories extracted from a fixed point located within an originally rose apple-dominated stand further supported these observations (Fig. 2). A marked shift occurred in 2019,

characterized by a reduction in near-infrared (NIR) reflectance together with an increase in shortwave infrared (SWIR) reflectance. A decrease in NIR reflectance typically signals a disruption in leaf cellular structure and a decline in chlorophyll content, while an increase in SWIR reflectance is commonly associated with water stress. Additionally, changes in leaf composition may also influence reflectance in the SWIR region. Hence, the observed combination of decreased NIR and increased SWIR is consistent with reduced canopy integrity and increased vegetation water stress. By 2024, although the stress signature no longer reflected severe physiological stress, it remained clearly distinct from that of the original rose apple canopy, indicating that the forest had largely been replaced by other vegetation types in the studied area.

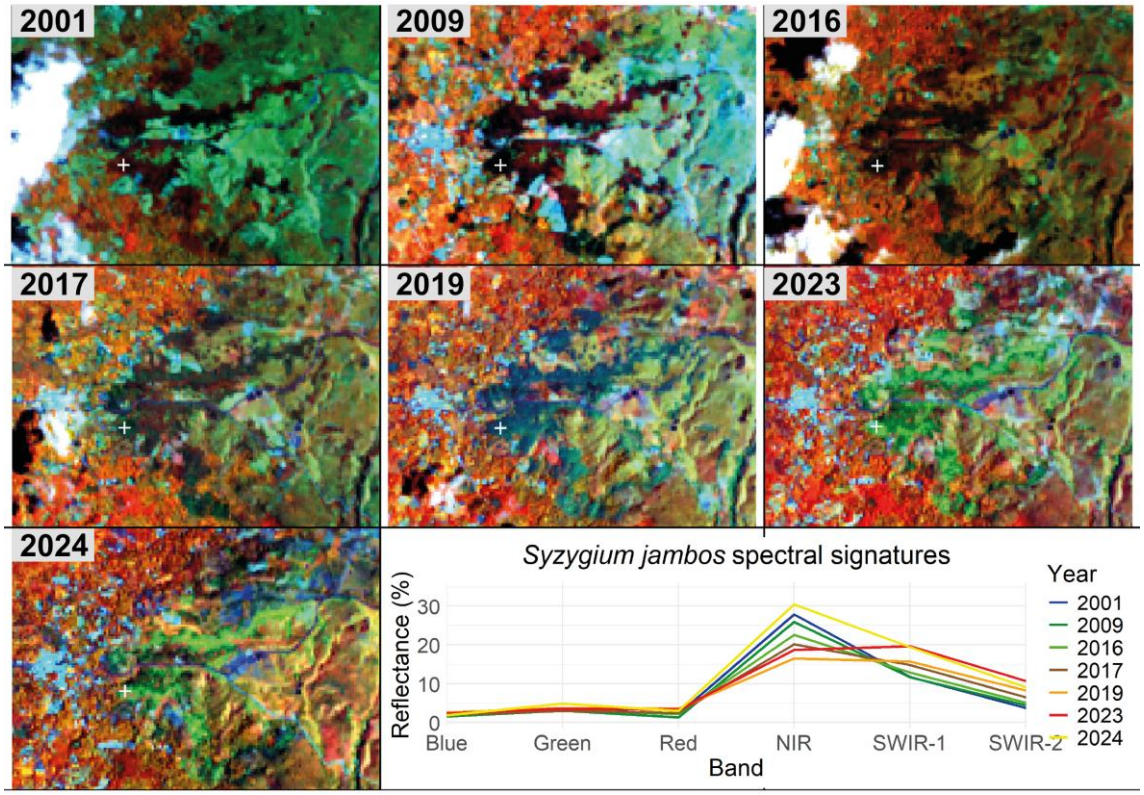


Fig. 2 Spectral patterns of *Syzygium jambos* within the San Cristóbal study area. False-color Landsat composites (RGB: NIR-SWIR-Red) for selected years illustrating progressive canopy decline. The white cross in each image indicates the fixed site from which reflectance curves were extracted for temporal analysis

Rapid contraction of *S. jambos* forest cover

Spatial classification of PlanetScope satellite imagery using the ISODATA algorithm revealed a dramatic reduction in the extent of *S. jambos* forest over the study period (Fig. 3). In 2018, the rose apple stands occupied approximately 278 ha within the San Cristóbal study area. By 2023, rose apple forest cover had declined to approximately 179 hectares, representing a loss of nearly 100 ha over five years. By 2024, only about 75 ha of *S. jambos* forest remained, corresponding to an overall decline of approximately 73% relative to its extent in 2018.

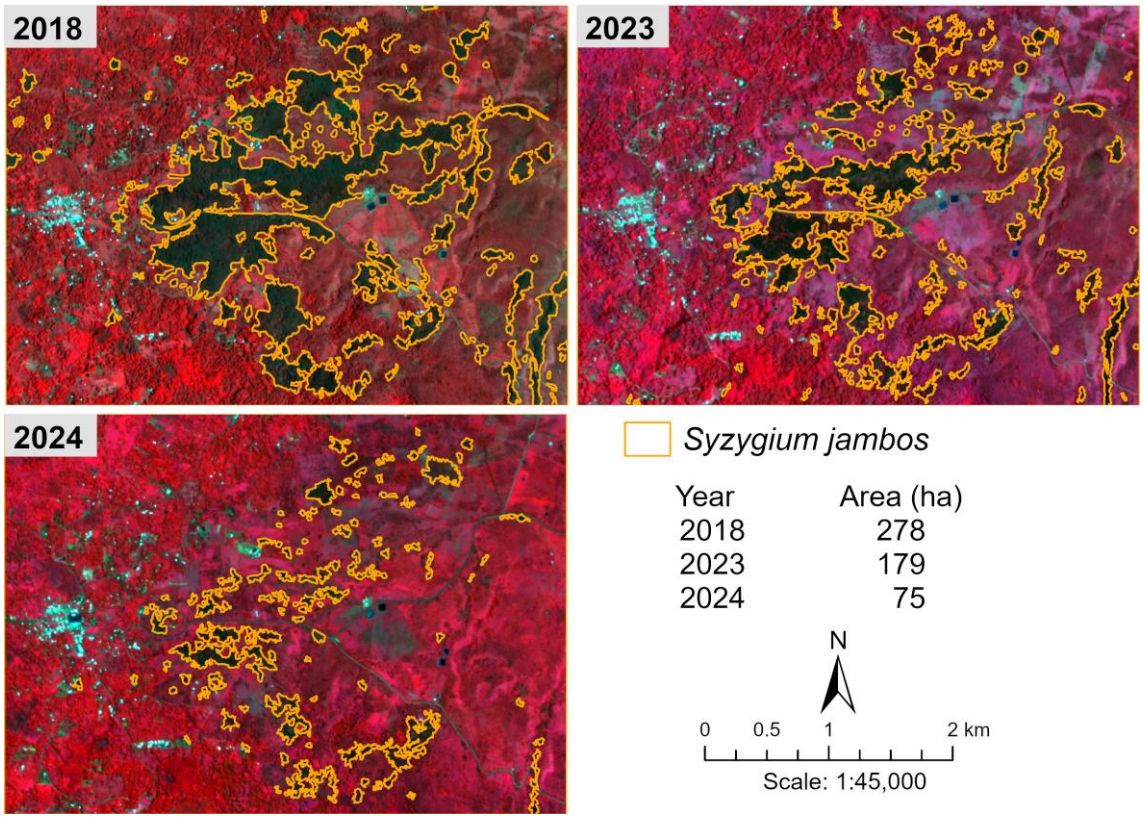


Fig. 3 Spatial distribution of *Syzygium jambos* forest in the San Cristóbal study area derived from ISODATA classification of PlanetScope satellite imagery. Maps illustrate the progressive reduction in forest cover between 2018 and 2024

Disease progression and morphological identification of the rust pathogen

Field observations documented a striking progression of disease symptoms in rose apple on San Cristóbal Island between 2019 and 2024 (Fig. 4a,b), with severely affected trees exhibiting extensive canopy decline, branch dieback, and severe defoliation. Close examination of infected leaves revealed characteristic rust symptoms, including bright yellow pustules surrounded by chlorotic tissue that later developed reddish-purple discoloration (Fig. 4c). Stereomicroscopy showed abundant, well-defined uredinial pustules distributed across the leaf surface (Fig. 4d).

Microscopic examination of fungal structures revealed abundant urediniospores that were bright yellow, globose to ellipsoidal or ovoid in shape, finely echinulate, with or without a tonsure, measuring approximately 18.9 to 28.2 µm in length and 12.8 to 20.6 µm in width (Fig. 4e). Teliospores were yellowish-brown, cylindrical to ellipsoidal in shape, one septate with rounded apices, measuring approximately 37.9 to 48.6 µm in length and 16.3 to 22.0 µm in width (Fig. 4f). These morphological characteristics are consistent with previous descriptions of the myrtle rust pathogen *Austropuccinia psidii* (Simpson et al. 2006).



Fig. 4 Disease progression and morphological characterization of rust infection caused by *Austropuccinia psidii* on *Syzygium jambos* in the Galápagos Islands. **(a,b)** Progression of myrtle rust symptoms on *S. jambos* plants in 2019 **(a)** and 2024 **(b)**. **(c)** Infected leaf showing characteristic rust symptoms with yellow uredinial pustules and surrounding chlorosis. **(d)** Stereomicroscopic image of uredinia on the leaf surface. **(e)** Microscopic view of urediniospores at 100× magnification. (**f)** Microscopic view of teliospores at 40× magnification

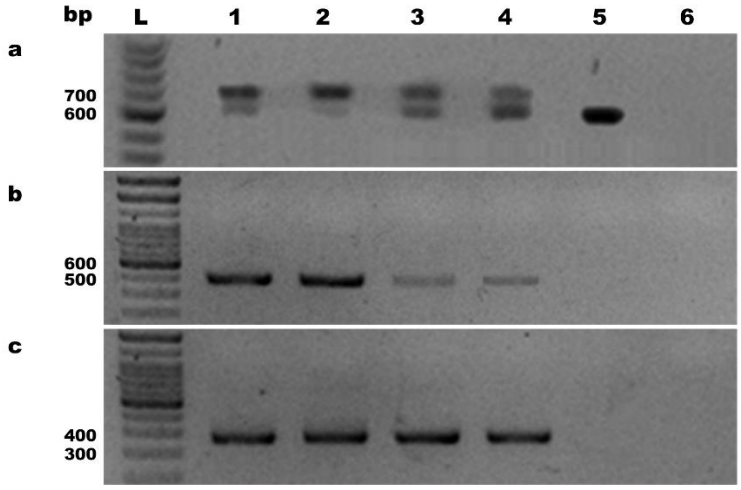


Fig. 5 Molecular detection of *Austropuccinia psidii* from infected *Syzygium jambos* leaves. PCR amplification of DNA extracted from spore washings (lane 1), fungal scrapings (lane 2), and infected leaf tissue (lanes 3 and 4), together with a *Fusarium triseptatum* DNA control (lane 5) and no-template control (lane 6). **(a)** Amplification with universal fungal primers ITS1F/ITS4. **(b)** First-round PCR with *A. psidii*-specific primers Ppsi1/Ppsi6. **(c)** Nested PCR with primers Ppsi2/Ppsi4. L, 100-bp DNA ladder used as size marker

PCR amplification with the universal fungal primers ITS1F and ITS4 yielded PCR products of approximately 600-700 bp for all DNA samples, confirming that the extracted DNA was suitable for downstream analysis (Fig. 5a). Although double bands were observed in several samples, amplification was successful for all samples except the no-template control.

The first-round PCR using primers Ppsi1 and Ppsi6 generated a single amplicon of approximately 500 bp, corresponding to the expected size (Fig. 5b). Nested PCR with *A. psidii*-specific primers Ppsi2 and Ppsi4 generated the expected product of approximately 370 bp in all infected samples, providing further evidence for the presence of *A. psidii* (Fig. 5). *Fusarium triseptatum* DNA was used as a positive control for amplification with the ITS primers but did not produce amplicons with either of the *A. psidii*-specific primer sets, consistent with their specificity.

The nested PCR products amplified with primers Ppsi2/Ppsi4 from the four infected samples were sequenced and compared against the NCBI database using BLASTn. All sequences matched to *A. psidii*, including a reference recorded under its synonym *Puccinia psidii*, with sequence identities ranging from 96.67% to 100% and 100% query coverage for all four samples. Details of the BLAST alignment results and percentage sequence identities are provided in Table S2. Accession numbers assigned to the sequences generated in this study are PX048491, PX048505, PX048506, and PX048507 for samples 1–4, respectively.

Discussion

In this study, the integration of remote sensing, field observations, and pathogen identification provides compelling evidence that the widespread decline of invasive rose apple trees on San Cristóbal Island is associated with severe infection by the invasive myrtle rust fungus *A. psidii.* Together, these complementary approaches document the rapid deterioration of invasive rose apple stands and place the confirmed presence of *A. psidii* within the context of landscape-scale changes in host cover in the Galápagos Islands.

Multispectral analysis detected a progressive shift in the spectral signature of rose apple tree stands, characterized by lower NIR reflectance and higher SWIR reflectance in 2019 and 2023 compared with the earliest observations. Such changes are widely recognized as indicators of declining canopy vigor, reflecting alterations in leaf internal structure, reduced water content, and changes in biochemical composition (Liu et al. 2014; Neuwirthová et al. 2017). Additionally, the edge-to-interior pattern, reflected

in the color shift described in the results section, is consistent with well-documented edge effects in fragmented forests, where microclimatic exposure, such as wind, light, and desiccation, makes edge trees more susceptible to disturbance and mortality than interior stands (Murcia 1995). These spectral images were accompanied by a 73% reduction in rose apple tree cover between 2018 and 2024, indicating extensive loss and fragmentation of rose apple stands. The close agreement between the remotely sensed patterns and field observations demonstrates the value of multitemporal satellite imagery for monitoring canopy decline associated with pathogen occurrence, particularly in remote island ecosystems where continuous field surveys are logistically challenging.

The observed decline may have been influenced by the strong El Niño events of 2015-2016 and 2023-2024, which can produce unusually warm and wet conditions across the Galápagos (NOAA 2026; Orellana-Samaniego et al. 2026). Climatic anomalies associated with El Niño are known to influence both host susceptibility and pathogen development, potentially accelerating disease outbreaks through increased plant stress and favorable conditions for pathogen infection and sporulation (Singh et al. 2023). Although our study does not establish a causal relationship between El Niño and the decline of *S. jambos*, these climatic events may have facilitated disease development and accelerated canopy deterioration. The observed decline is therefore most likely the result of interacting biotic and abiotic drivers rather than a single causal factor.

Field observations documented a dramatic increase in disease severity between 2019 and 2024, with extensive canopy dieback, defoliation, and abundant rust pustules on infected leaves. The morphology of urediniospores and teliospores closely matched previous descriptions of *A. psidii* (Simpson et al. 2006), while species-specific nested PCR and sequence analysis independently confirmed the identity of the pathogen. Together, these findings support the association of *A. psidii* with the rust disease observed on invasive *S. jambos* on San Cristóbal. Morphological and molecular identification of the same host–pathogen association in Galápagos was also described in a manuscript recently made available on agriRxiv, CABI's preprint repository (Pineida et al. 2026). Given the efficient wind dispersal of urediniospores, the potential for rapid spread of the pathogen throughout dense rose apple stands is consistent with the observed progression of disease (Uchida and Loope 2009). However, these observations do not establish the extent to which rust infection contributed to the landscape-scale decline of *S. jambos*, and the relative contributions of the pathogen and other biotic or abiotic factors remain unresolved.

Beyond documenting a host-pathogen association in the Galápagos, our findings illustrate a broader ecological process in biological invasions. The remarkable success of invasive rose apple following its introduction to the Galápagos is consistent with the Enemy Release Hypothesis, which proposes that introduced species gain a competitive advantage by escaping the specialist herbivores and pathogens that regulate their populations in their native range (Keane and Crawley 2002). However, the occurrence of *A. psidii* on *S. jambos* is consistent with the hypothesis that invasive plants may acquire pathogens in their introduced range, potentially reducing their competitive advantage. Such delayed acquisition of natural enemies has been proposed as an important mechanism contributing to the long-term regulation of invasive plant populations and may partly explain the rapid decline of *S. jambos* observed in this study (Flory et al. 2011).

The route by which *A. psidii* reached the Galápagos remains unknown, although accidental introduction through infected plant material or contaminated propagules represents a plausible scenario (Pegg et al. 2014). The introduction of a pathogen can create novel interactions with native hosts that lack a shared coevolutionary history, potentially increasing their susceptibility to infection (Desprez-Loustau et al. 2007). However, disease emergence also depends on host–pathogen compatibility and suitable environmental conditions, so introduction may not immediately lead to an evident disease outbreak (Parker and Gilbert 2004). Following introduction, the extensive distribution of rose apple may have provided a large, continuous, and highly susceptible host that facilitated pathogen establishment and spread. Similar delayed disease outbreaks have been described for other invasive host-pathogen systems, where pathogen populations remain undetected until ecological or climatic conditions become favorable for epidemic development (Parker and Gilbert 2004; Flory and Clay 2013; Velásquez et al. 2018). Resolving the origin and invasion history of *A. psidii* in the Galápagos will require population genomic analyses comparing isolates from the archipelago with those from potential source regions.

From a conservation perspective, our findings highlight an ecological paradox: an invasive fungal pathogen infecting an invasive tree in a vulnerable island ecosystem. The approximately 73% reduction in *S. jambos* forest cover between 2018 and 2024, together with observations of widespread rust infection, suggests that interactions among non-native species may influence invasion dynamics. We hypothesize that the accumulation of introduced species in the Galápagos may create opportunities for novel ecological interactions, including associations between introduced plants and pathogens. Such interactions could contribute to the suppression of invasive plants while generating additional risks to native biodiversity. In this case, the decline of rose apple may create opportunities for native vegetation recovery, but *A. psidii* is not restricted to *S. jambos*: it infects a broad diversity of Myrtaceae and has caused severe disease outbreaks in South America, Australia, and Hawaii (Uchida and Loope 2009). Its presence may therefore pose a threat to native and endemic Galápagos Myrtaceae, including *Psidium galapageium*, as well as agronomically important introduced species such as *Psidium guajava* (Urquía et al. 2019).

The potential dual role of *A. psidii* illustrates the complexity of pathogen invasions on oceanic islands. While the pathogen may indirectly benefit ecosystem restoration by suppressing an aggressive invader, it may also pose a novel disease risk to native biodiversity. The decline of one invasive species through its interaction with another invader therefore does not necessarily represent an ecological victory. Future research should prioritize island-wide surveillance of Myrtaceae, assessments of endemic species' susceptibility, and long-term monitoring of vegetation dynamics to determine whether the decline of *S. jambos* facilitates ecosystem recovery or is accompanied by broader disease impacts on the archipelago's unique flora.

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Statements and Declarations

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Data availability The sequences generated from nested PCR products amplified with primers Ppsi2/Ppsi4 are available in GenBank under accession numbers PX048491, PX048505, PX048506, and PX048507. Additional data supporting the findings of this study are provided in the article and its Supplementary Information.

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