



Climate change facilitates fungal pathogen expansion while driving endemic host range contractions in a tropical biodiversity hotspot

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Abstract

Context Non-native plant pathogens are reshaping ecosystems globally, yet their spread and potential spatial distributions under future climate and land cover change remains underexplored, particularly in biodiversity hotspots with vulnerable hosts. In Madagascar, a vascular wilt pathogen (*Leptographium calophylli*) has been increasingly observed infecting native forest trees raising conservation concerns.

Objectives We aimed to model future distributions of both a vulnerable host tree *Calophyllum paniculatum* and incipient wilt pathogen *Leptographium*

calophylli under climate and land cover change scenarios over the next 80 years to assess potential for overlap, divergence, and implications for extinction risk.

Methods Using ensemble SDMs across Madagascar, we forecasted potential distributional ranges for both pathogen and host using the Global Climate Model (GFDL-ESM4) under three scenarios (SSP1–2.6, SSP3–7.0, SSP5–8.5) and time periods (2011–2040, 2041–2070, 2071–2100). We measured future range shifts using a habitat exposure index and potential area of occupancy.

Results The pathogen is predicted to retain 68.5% of the current projected distribution by 2100, with expansion into previously uninhabited regions. *C. paniculatum* is forecast to experience range contraction (65.9% loss by 2100) with persistent distributional overlap predicted across all scenarios.

Conclusion We demonstrate that future climatic conditions may facilitate fungal pathogen expansion, while simultaneously exposing vulnerable hosts within their native, endemic range to infection. The asymmetric dynamic of host range losses could intensify biodiversity loss in insular ecosystems, particularly when compounded by deforestation. This study highlights the importance of considering disease threats in biodiversity forecasts and conservation strategies, particularly in tropical systems facing rapid environmental change.

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Introduction

Emerging plant pathogens are increasingly recognised as a major driver of biodiversity loss (IPBES 2023). In tropical island hotspots, where host species are endemic, often range-restricted, ecologically specialised and already stressed by habitat loss and climate change (Brown, 2022), pathogen invasion can have profound consequences. In such systems, pathogen-driven mortality of dominant or functionally unique trees can rapidly alter community structure and ecosystem function, potentially triggering local extinctions and cascading ecological consequences (Boyd et al. 2013). For instance, such infections can truncate seed-shadow and recruitment by removing parent trees (Augspurger and Wilkinson 2007), reduce fruit and nectar availability that in-turn depress frugivores and pollinators (Razafindratsima et al. 2014), diminish above-ground carbon stocks (Slik et al. 2013), and alter litter inputs (Fonte and Schowalter 2004). In combination, these impacts can shift community composition toward disturbance-tolerant states (e.g., liana-dominant, (Visser et al. 2018) and heighten fire susceptibility at forest margins (Metz et al. 2011). These changes are difficult to reverse once thresholds are crossed (Reyer et al. 2015). Consequently, as global change intensifies, understanding how plant-pathogen dynamics may progress temporally and spatially becomes central to predicting and mitigating biodiversity loss.

Climate change influences host–pathogen interactions through changes in temperature and moisture regimes that govern pathogen sporulation, infection efficiency and survival (Elad and Pertot 2014; Garrett et al. 2006), as well as host stress and defence (Desprez-Loustau et al. 2007; Sturrock et al. 2011). Depending on the pathogen-host system, warming, altered precipitation and seasonality patterns may facilitate pathogens to track hosts and expand into previously unoccupied refugia (Bebber et al. 2013). Conversely, some pathogens might encounter environmental thresholds that limit their survival and spread, thereby creating spatial refugia for host species. The development of robust disease risk models that forecast pathogen distribution under altered

climatic conditions is therefore crucial, not only for predicting disease outbreaks but also for informing effective conservation strategies and management practices in vulnerable ecosystems.

Many conservation strategies in invasion ecology rely on correlative species distribution models (SDMs) to predict how species' ranges may shift in response to environmental change. These SDMs are widely used to identify climate refugia and prioritise conservation strategies (Li and Wang 2013; Peterson et al. 2012). However, most SDMs focus solely on abiotic variables and assume species respond independently to environmental gradients. This assumption breaks down when biotic factors, such as host–pathogen dynamics, and human-led dispersal shape a species' realised niche, e.g., taking consideration of the 'BAM' framework (Escobar and Craft 2016; Soberón, 2005). For host species facing pathogen pressure, projected range shifts may not reflect future viability if pathogens are able to track or outpace hosts. Conversely, if pathogen ranges contract or shift differently than their hosts, it may result in spatial refugia for the host species, potentially increasing their resilience. These outcomes have fundamentally different implications for extinction risk, yet few SDM-based conservation studies consider such spatial overlap explicitly (Goberville et al. 2016; Sopniewski et al. 2022).

Critically, this omission may lead to over-optimistic or misleading conservation assessments. Yet the methodological and data challenges of mapping host and pathogen together are considerable, especially for under-studied species in poorly sampled regions. These knowledge gaps are particularly stark in tropical island ecosystems, where high rates of endemism intersect with high vulnerability to invasive species, habitat loss and climate change (Bellard et al. 2017; Dawson et al. 2017). Madagascar is emblematic of this convergence. The island harbours exceptional biodiversity, including over 12,000 plant species, of which 83% are endemic (Goodman 2023). Yet this richness coexists with accelerating environmental degradation: deforestation, driven by slash-and-burn agriculture and fuelwood harvesting, has already reduced the country's natural forest cover to less than 10% of its original extent (Harper et al. 2007; Vieilledent et al. 2018). Concurrently, climate models forecast substantial shifts in temperature and precipitation

patterns across the island (Brown, 2022; Goodman 2023). These stressors interact with increasing biotic pressures, including the incipient introduction of pathogens not previously known to occur in these systems. However, the extent to which disease dynamics will interact with climate and land cover change to reshape species distributions in Madagascar remains largely unknown.

One illustrative example is the recently described vascular wilt disease affecting native, endemic *Calophyllum* species in Madagascar. The fungal pathogen thought to be *Leptographium calophylli* (formerly *Verticillium*) has been observed causing mortality in *C. paniculatum*, *C. drouhardii*, and *C. milvum* populations in Ranomafana National Park since 2016 (Wright et al. 2020). Although *Leptographium* species are globally distributed and known to cause disease in other woody hosts, their ecology and epidemiology in Madagascar's forests remain poorly characterised. The origins of this outbreak are uncertain, which underscores the urgency of proactive monitoring and spatial forecasting under future environmental change.

To address these ecological knowledge gaps, we use ensemble SDMs to model current and future suitability for both the vascular wilt pathogen (*Leptographium calophylli*) and a susceptible endemic host (*Calophyllum paniculatum*) across Madagascar under three climate and deforestation scenarios, at three future time slices. The overarching aim of this study is to identify persistent risk hotspots and candidate refugia to inform conservation prioritisation and provide a template for data-poor tropical ecosystems. For the final research objective, we will map host–pathogen spatial coupling and identify mortality and risk hotspots by deriving overlap, divergence and elevational range metrics to classify regions of intensified exposure and potential refugia. One plausible outcome is partial decoupling with persistent overlap, for example, if pathogen suitability remains relatively stable while the host contracts or shifts differently in space or elevation, yielding refugia alongside enduring co-occurrence and sustained mortality risk. The alternatives are equally plausible: (i) tight coupling if both taxa track similar directional and elevational shifts, maintaining high overlap of predicted presence; (ii) risk attenuation if pathogen predicted distributions contract or shift away faster than the host, enlarging refugia; or (iii) risk escalation if pathogen

predicted presence expands or shifts faster than the host, increasing exposure.

Materials and methods

We chose to accompany this methods section with Overview, Data, Model, Assessment and Prediction (ODMAP) protocols and full code for each species modelled (Zurell et al. 2020) in the name of openness and transparency (<https://github.com/GeoEma/Underwood-fungal-host-SDMs-2026>). These protocols summarise all parameter decisions and inputs made to build and predict future range shifts of both the focal tree and its wilt pathogen.

Study site

Madagascar (and Indian Ocean Islands) is one of 36 global biodiversity hotspots, combining exceptional endemism with extensive habitat loss (Mittermeier et al., 2011). The island lies *ca.* 90 km east of mainland Africa (Fig. 1, extent A) and has lost much of its natural forest cover to deforestation and degradation, primarily through shifting agriculture and fuelwood extraction (Brown, 2022; Goodman 2023; Harper et al. 2007; Vieilledent et al. 2013).

Because the focal non-native fungal pathogen – *Leptographium calophylli* – has not yet been systematically recorded in Madagascar but has a documented history on neighbouring Indian Ocean islands and mainland Africa (Webber et al. 1999; Wiehe 1949), we treated continental Africa as the putative source region and Madagascar as the potential invasion front. We therefore defined two raster extents at 1-km resolution (Fig. 1): (i) a training extent covering mainland Africa (extent A) used to model the pathogen's climatic niche based on African occurrences and (ii) a projection extent covering Madagascar (extent B) where we projected both pathogen and endemic host suitability through time. Raster templates for both extents were prepared using Global Administrative Areas (GADM.org) data, including only mainland extents and excluding coastal islands to avoid artefacts along shorelines. Ranomafana National Park (extent B) was highlighted as the location where wilt symptoms on *Calophyllum* species were first reported and monitored (Wright et al. 2020), providing an independent reference for

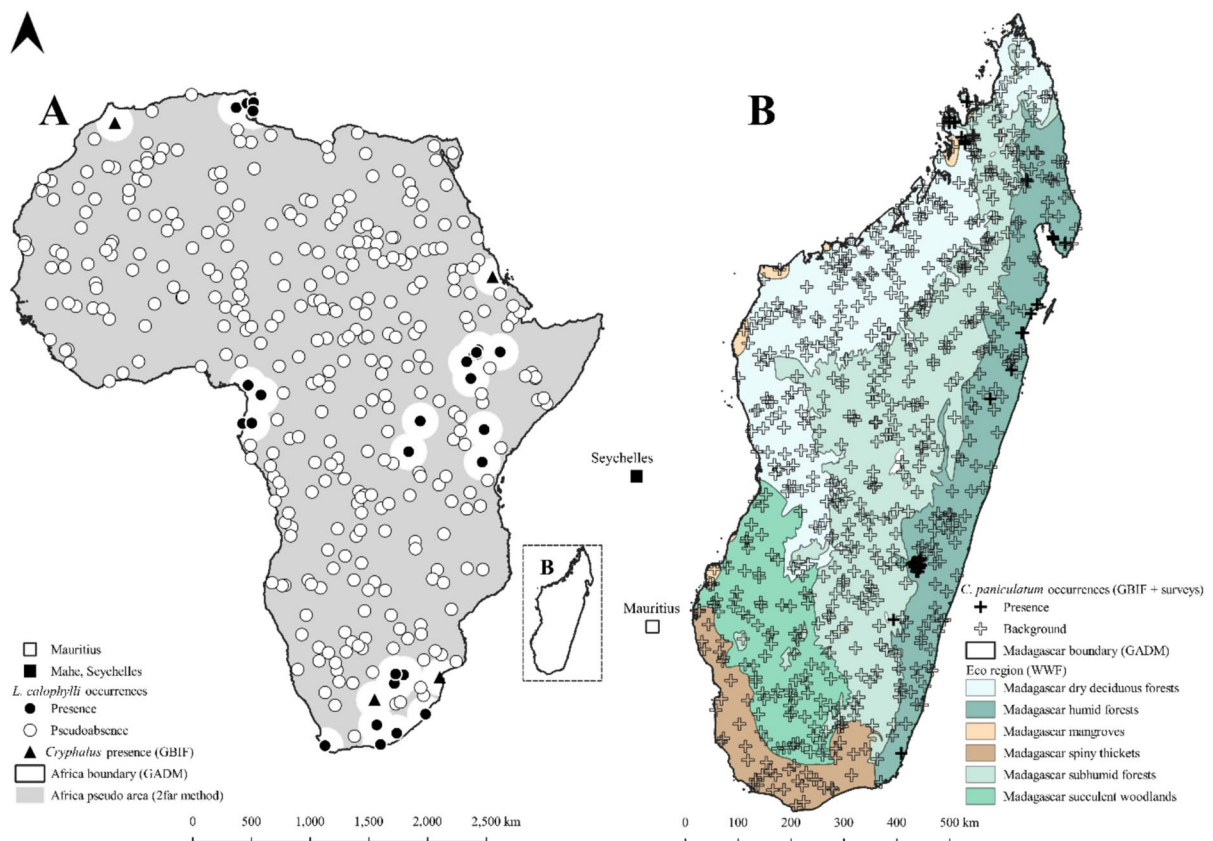


Fig. 1 Map of Africa showing the training extent (A) for the fungal wilt pathogen *L. calophylli* SDM at 1 km spatial resolution. Madagascar (B) is the prediction extent where both the fungal wilt pathogen *L. calophylli* and host tree distributions were mapped in time and space. *Verticillium* and *Lep-tographium* occurrences were downloaded and cleaned from GBIF (2025a) to represent the wilt pathogen *L. calophylli* ($n=34$), and field surveys bolstered further GBIF occurrences of the host tree ($n=62$) *C. paniculatum* (Armstrong et al. 2018; GBIF 2025b; Ramananjato, 2021; Ramananjato and Razafindratsima 2021a, b; Rovero and Ahumada 2017).

Ranomafana National Park, shown by clustered presence of *C. paniculatum* in the south-eastern humid forest was the first recorded sighting of *L. calophylli* (Wright et al. 2020). Pseudo-absences were randomly generated for the wilt pathogen which excluded a set distance from pathogen (black circles) and *Cryphalus* bark beetle dispersal vector occurrences (triangles) (Barbet-Massin et al. 2012; GBIF 2025c). Seychelles (grey square) and Mauritius (black square) are also identified as nearby islands of known pathogen spread sightings (Webber et al. 1999; Wiehe 1949)

evaluating projected establishment and subsequent invasion potential from SDM predictions.

Study species

Endemic host plant

Calophyllum is a genus of evergreen tropical trees in the family Calophyllaceae (formerly “Clusiaceae”), comprising 87 recognised species globally (IUCN 2023). Many species in the genus show negative population trends, with 29% assessed as

decreasing and 57% are data deficient (IUCN 2023). *Calophyllum paniculatum* P.F. Stevens (hereafter *C. paniculatum*) is endemic to mid-level elevation humid and sub-humid ecoregions of Madagascar, where it forms part of the canopy in evergreen rainforests. It is currently categorised as vulnerable on the IUCN Red List (IUCN 2019), and recent reports of high adult mortality associated with the vascular wilt (Wright et al. 2020), raise concern that climate change, land cover change and pathogen invasion may interact to accelerate its decline.

Fungal wilt pathogen

A vascular wilt disease has been causing increasing adult mortality in *C. paniculatum* in Ranomafana National Park since 2016 and is attributed to a fungal pathogen in the genus *Leptographium*, most likely *Leptographium calophylli* (*L. calophylli*) (Wright et al. 2020). The fungal wilt *L. calophylli* has long been recognised as a serious pathogen of *Calophyllum* trees in other tropical and subtropical moist broadleaf biomes in the Indian Ocean islands of Seychelles and Mauritius (Wainhouse et al. 1998; Webber et al. 1999; Wiehe 1949). In addition, it was documented from *C. brasiliense* var. *rekoi* in culture collections from El Salvador (Crandall 1949). The external symptoms include rapid crown wilting and canopy dieback, while internally the disease is characterised by dark brown vascular streaking visible in the xylem tissue (Wiehe 1949; Wright et al. 2020). Evidence confirming host specificity remains limited, largely because it is difficult to determine conclusively (Cheng and Yu 2025). However, recent observations from the latest outbreak in Ranomafana National Park, Madagascar, recorded visible external symptoms in *Calophyllum* stands (Wright et al. 2020). Nevertheless, asymptomatic hosts may still facilitate pathogen dispersal across the landscape (Prospero and Cleary 2017). In our study, we therefore assume that the modelled pathogen can survive and disperse without specific *Calophyllum* species, based on available Global Biodiversity Information Facility (GBIF) records in Africa (GBIF 2026).

Dispersal vector

Although aerial dispersal of spores may only contribute locally, long distance spread of *L. calophylli* across islands separated by hundreds of kilometres is likely to have been facilitated by human movement of infected timber. An ecologically important vector for the dispersal within forests is the bark beetle, *Cryphalus* Erichson, 1836. This genus of beetle range in size from 0.8–3 mm in length and inhabit tree bark where fungal spores attach to their exoskeleton and are transported to new hosts (Wainhouse et al. 1998). At least 25 *Cryphalus* species occur on the African Continent (GBIF 2025c) and *Cryphalus trypanus* has been identified as the principal vector of the

Calophyllum wilt pathogen in Seychelles and Mauritius (Wainhouse et al. 1998).

Occurrence records

To our knowledge, there are no officially reported, geolocated occurrences of the fungal wilt *L. calophylli* in Madagascar in any global biodiversity database, aside from surveys from Ranomafana National Park (Fig. 1, extent B; Wright et al. 2020). Due to recent taxonomic and historical uncertainty surrounding the fungal pathogen's identity (Wainhouse et al. 1998; Webber et al. 1999; Wiehe 1949), we broadened our query to the wilt genera *Verticillium* Nees, 1816 and *Leptographium* Lagerb. & Melin. All records for these genera restricted to mainland Africa (Fig. 1, extent A) were downloaded from GBIF (GBIF 2025a). We removed records with missing, inconsistent, or obviously incorrect geographic coordinates and excluded records with zero counts. The initial dataset comprised *Leptographium* (n=10) occurrences from southern Africa and *Verticillium* (n=86) occurrences from northern, western, and eastern Africa. After thinning spatial duplicates within 1 km grid cells, n=34 unique fungal wilt occurrences remained. For simplicity, we refer to these general-level occurrences as *L. calophylli*.

For the endemic host plant *C. paniculatum*, we again, collated all records (n=65) with accepted coordinates (GBIF 2025b) and supplemented these with field observations from multiple surveys in Madagascar, including the Tropical Ecological Assessment and Monitoring (TEAM) network (Rovero and Ahumada 2017), Centre ValBio (CVB) wilt surveys (Wright et al. 2020), a microhabitat study (Ramananjato, 2021; Ramananjato and Razafindratsima 2021a, b) and a soil survey in which the host was recorded as present (Armstrong et al. 2018). To minimise temporal duplication, we retained one record per plot for a common survey year (2018) within each dataset where appropriate. This yielded a final set of 62 unique *C. paniculatum* occurrences for terrestrial Madagascar (Fig. 1, extent B).

To accompany the collated species presence points within the ensemble modelling framework, pseudo-absences and background points were generated then combined with the presence data for the wilt and host. After initial sensitivity testing of each method which explored multiple methods, the fungal wilt

pseudoabsences were constructed using the ‘2° far’ buffer approach (Fig. 1, extent A (Barbet-Massin et al. 2012)), where following Li et al. (2024), we also combined presence records for the bark beetle vector *Cryphalus* (Fig. 1, extent A) obtained from GBIF and grouped with the fungal wilt occurrences (GBIF 2025c). We chose to generate pseudoabsences rather than background points to explicitly contrast presence and absence environments across the wide environmental gradients of Africa (Barbet-Massin et al. 2012). This approach is appropriate when occurrence data are suspected to be incomplete and spatially biased (Phillips et al. 2009), as is typical for fungal pathogens in GBIF where sampling is constrained by accessibility and the cryptic nature of the species (Boria et al. 2014). Host background points were randomly generated across the whole of Madagascar after testing showed this outperformed a targeted ecoregion background approach. For more information, see Online Resource 1, 2 and 3.

Environmental information

To characterise contemporary and future macroclimate, we extracted bioclimatic variables from *CHELSA* v2.1 (Karger et al. 2017, 2021), at each occurrence location. These represent the 19 standard temperature and precipitation predictors at 30 arc-seconds (~1 km at the equator) spatial resolution. These variables capture seasonal variability and extremes to constrain tropical tree distributions and fungal pathogen dynamics. We extracted climate projections from the CMIP6 GFDL-ESM4 general circulation model under three Shared Socioeconomic Pathway scenarios: SSP1-RCP2.6, SSP3-RCP7, and SSP5-RCP8.5 (Krasting et al. 2018), spanning low, medium and high emissions futures and thus bracketing plausible climates that could mediate both host range shifts and climate-facilitated pathogen invasion. We assembled these variables across four time periods: 1981–2010 (current baseline), 2011–2040, 2041–2070 and 2071–2100. In addition, we included forest cover projections from the *ForestAtRisk* model for Madagascar (Vieilledent 2021; Vieilledent et al. 2018). *ForestAtRisk* provides 30 m resolution maps of historical forest cover and projected deforestation under a “business as usual” scenario with baseline data for 2010–2020 and projections for 2040, 2070, and 2100

aligned with our climate time slices. These projections suggest that, under continued deforestation, humid forest in Madagascar could be almost entirely lost by 2100, with large uncertainty in the exact timing of collapse but consistent trends of decline across scenarios (Vieilledent et al. 2018). These combined data represented temporally matched, dynamic forest cover layers that were used as a proxy for intact humid and sub-humid forest structure relevant to host *C. paniculatum* establishment.

Species distribution modelling (SDM)

We used ensemble species distribution models (SDMs) to relate species occurrences to climatic and land-cover variables and to project habitat suitability under future scenarios (Araújo and New 2007). Our framework models an emerging fungal wilt (*L. calophylli*) and its endemic host tree *C. paniculatum* to: (i) characterise their current environmental niches, (ii) forecast potential invasion and range shifts under combinations of climate change and deforestation and (iii) quantify changing spatial overlap between pathogen and host. In the context of Madagascar’s endemic flora, these models provide an effective way to explore how climate-mediated pathogen invasion could interact with ongoing habitat loss to reshape host distributions and extinction risk.

Predictor variable selection

We restricted SDM complexity and minimised multicollinearity among predictors to avoid overfitting (Dormann et al. 2013). Initially, we considered the 19 *CHELSA* bioclimatic variables and *ForestAtRisk* forest cover, then quantified collinearity separately for the pathogen (African training extent) and host (Madagascar) datasets using Spearman’s rank correlation matrices and Variance Inflation Factors (VIF). Highly correlated pairs ($|r| \geq 0.7$) were identified and one variable from each pair was removed based on their VIF, yielding a pool of non-collinear predictors for each species (Online Resource 4, Figures S2–3). To keep model complexity proportionate to sample size, we limited the number of climate predictors to approximately one variable per 8–10 presence records (Merow et al. 2013; Guisan and Zimmermann 2000).

This meant we could build models using six predictor variables for the host plant (*C. paniculatum*) and four for the fungal pathogen (*L. calophylli*). As this could result in an oversimplified model for the latter, we accounted for the sensitivity of model performance to various numbers of predictor variables and selection procedures in a preliminary analysis. Results highlighted the simple model, using just four climatic predictors as the best performing model (results not shown; tested methods are listed in the ODMAP protocol, Online Resources Tables 1 and 2).

For the fungal wilt pathogen, the final non-col-linear climate predictors were: (i) precipitation of the driest month, (ii) precipitation seasonality, (iii) mean temperature of the coldest quarter, and (iv) precipitation of the coldest quarter. Together, these variables captured dry-season moisture stress (Desprez-Loustau et al. 2007), intra-annual rainfall variability (Thompson et al. 2014) and cool season thermal (Aguayo et al. 2014) and moisture regimes (Burgess et al. 2017) that are known to constrain survival, overwintering and infection windows of vascular wilt fungi. For the endemic host tree, the final predictors comprised: (i) temperature seasonality, (ii) mean temperature of the driest quarter, (iii) annual temperature range, (iv) precipitation of the wettest month, (v) precipitation of the coldest quarter, and (vi) forest cover. These variables summarise thermal stability and extremes (Engelbrecht et al. 2007; Morellato et al. 2016; Park Williams et al. 2013), water availability during both wet and cool seasons (Esquivel-Muelbert et al. 2017; McDowell et al. 2020), and the presence of closed-canopy forest, consistent with *C. paniculatum* as a humid rainforest tree whose distribution is shaped by relatively stable tropical climates and the persistence of intact forest structure (De Moraes et al. 2006; Stevens 1980).

Ensemble model fitting and validation

We used a weighted ensemble approach to reduce bias from individual algorithms and better capture uncertainties in predictions across climate and deforestation scenarios (Araújo and New 2007; Thuiller et al. 2019). Ensemble models were built using the *sdm* R package (Naimi and Araújo 2016). For each species, we fitted three algorithms that perform well with limited occurrence data: Boosted Regression

Tree (BRT), Random Forest (RF) and MaxEnt (Williams et al. 2009). Models were replicated ten times for each algorithm using bootstrap resampling, producing 30 models *per* species in the final model. For each ensemble, to account for the much larger number of background data relative to presences, we applied a weighting ratio such that each pseudo-absence/background point contributed one-tenth of the weight of a presence, making the total weighted contribution of presences and pseudo-absences/background points approximately equal in each model replicate. We used five-fold cross-validation, with an 80:20 training–testing split in each fold (Araújo et al. 2005). Two- and three-dimensional partial response curves were generated for all predictors and suitability predictions were averaged across replicates and algorithms to obtain ensemble mean predictions for subsequent performance evaluation and projection (Online Resource 4, Figures S11–12).

Ensemble model performance evaluation

We assessed the performance of each individual model replicate using threshold-independent discrimination metrics: Area under the receiver operating curve (AUC), True Skill Statistic (TSS) and the standard deviation of both for each cross-validation fold (Allouche et al. 2006; Liu et al. 2013). The top trained ensembles were inspected for ecologically plausible response curves and spatial distribution patterns before being retained for future projections (Online Resource 4, Figures S4–5). For the final wilt ensemble, we chose Matthews Correlation Coefficient (MCC) as the primary evaluation metric due to its robustness in novel environmental conditions and effectiveness in handling class imbalance (Boughorbel et al. 2017). For the host tree *C. paniculatum*, the final ensemble used AUC-weighted averaging, further optimised with respect to maximising TSS to balance omission and commission errors.

For each species, we quantified variable importance for the top ensemble model by permuting predictors one at a time and measuring the resulting loss in predictive performance (Dormann et al. 2013). In the permutation approach, values of a given predictor were randomly shuffled across sites while all other predictors were kept unchanged, so the greater the reduction in model performance, the higher

the inferred importance of that predictor (Online Resource 4, Figures S9–10). Importance scores were averaged across algorithms within the top ensemble and rescaled to facilitate comparison among variables within each species (Naimi and Araújo 2016).

Thresholding to create binary presence/absence

To analyse future range shift and host–pathogen overlap, we converted continuous probability of presence maps (Online Resource 4, Figures S7–8) to binary presence-absence maps for each species, climate scenario and time period. We used the *threshold* function in the *sdm* R package to identify an optimal binary cut-off for each ensemble, weighting towards the best-performing algorithms and replicates. For the wilt pathogen *L. calophylli*, we used the minimum distance to ROC curve ("minROCdist") optimiser to improve transferability between Africa and Madagascar and reduce overprediction in novel climates (Owens et al. 2013). For the host tree *C. paniculatum*, modelled within its native range, we optimised the weighted ensemble towards the maximum sum of sensitivity and specificity ("max(se+sp)", or TSS) to balance omission and commission error rates (Liu et al. 2013). The binary maps were used to calculate distributional changes using area, centroid, altitudinal changes, as well as habitat exposure, and the predicted area of occupancy (pAOO), following Choe et al. (2017) and the IUCN (2022). See Online Resource 3, Figure S1.

Mapping novel environments and uncertainty

We performed a Multivariate Environmental Similarity Surface (MESS) analysis on the top ensemble for each species to assess the similarity between current and future climatic conditions (Elith et al. 2010; Zurell et al. 2012). Given the model transfer from Africa to Madagascar, this was particularly helpful to analyse any differences in conditions between training and testing (geographic disparity) as well as changes in environmental conditions over time across Madagascar between climate scenarios. In addition, we evaluated the spatial uncertainty of predictions, using high and low confidence presence and absence

categories, allowing for spatially explicit interpretation of model outputs mapped across Madagascar. For this, we used a percentile-based approach to threshold the uncertainty (entropy) layer created for each ensemble, using 75% and 25% as thresholds for high and low confidence, respectively (Thuiller et al. 2019). For high confidence predictions, we applied a threshold at the point where > 75% of models were in agreement for each pixel (the inverse of the entropy layer). The same was applied for low confidence predictions, where a threshold was chosen where < 25% of models agreed. We wrote custom code to make this process dynamic, testing 5% increments to account for any cases of high agreement across model algorithms and replicates in case the default resulted in a zero-value threshold. This ensured the uncertainty measurements were specific to each species and ensemble model.

Preliminary environmental data processing was carried out in QGIS (3.40 LTR). All further data preparation, modelling and analysis was performed using R Statistical Software (v4.3.2 (2023–10–31 ucrt); (R Core Team, 2023)) with packages *rgbif* (Chamberlain S, 2017; Chamberlain and Boettiger 2017) and *terra* (Hijmans 2025) for spatial data processing of pseudoabsences and background points. Further methods information is found in Online Resources 1 & 2 (ODMAP protocols).

Results

Projections of host pathogen distributions under current climate

When visualising current projections for the wilt pathogen *L. calophylli* (Fig. 2a), the pathogen is predicted to be present across a larger and overlapping geographic extent than host *C. paniculatum* (Fig. 2b). There are high confidence areas of suitable habitat across the entire north–south humid belt of the island, and high confidence absences to the west, largely encompassing the entire distribution of *C. paniculatum*, although the host distribution is sparser within the same humid and sub-humid belts. High confidence wilt suitability is projected for the independent reference area within Ranomafana National Park where the pathogen has been observed causing mortality to *C. paniculatum* since 2016. There are some

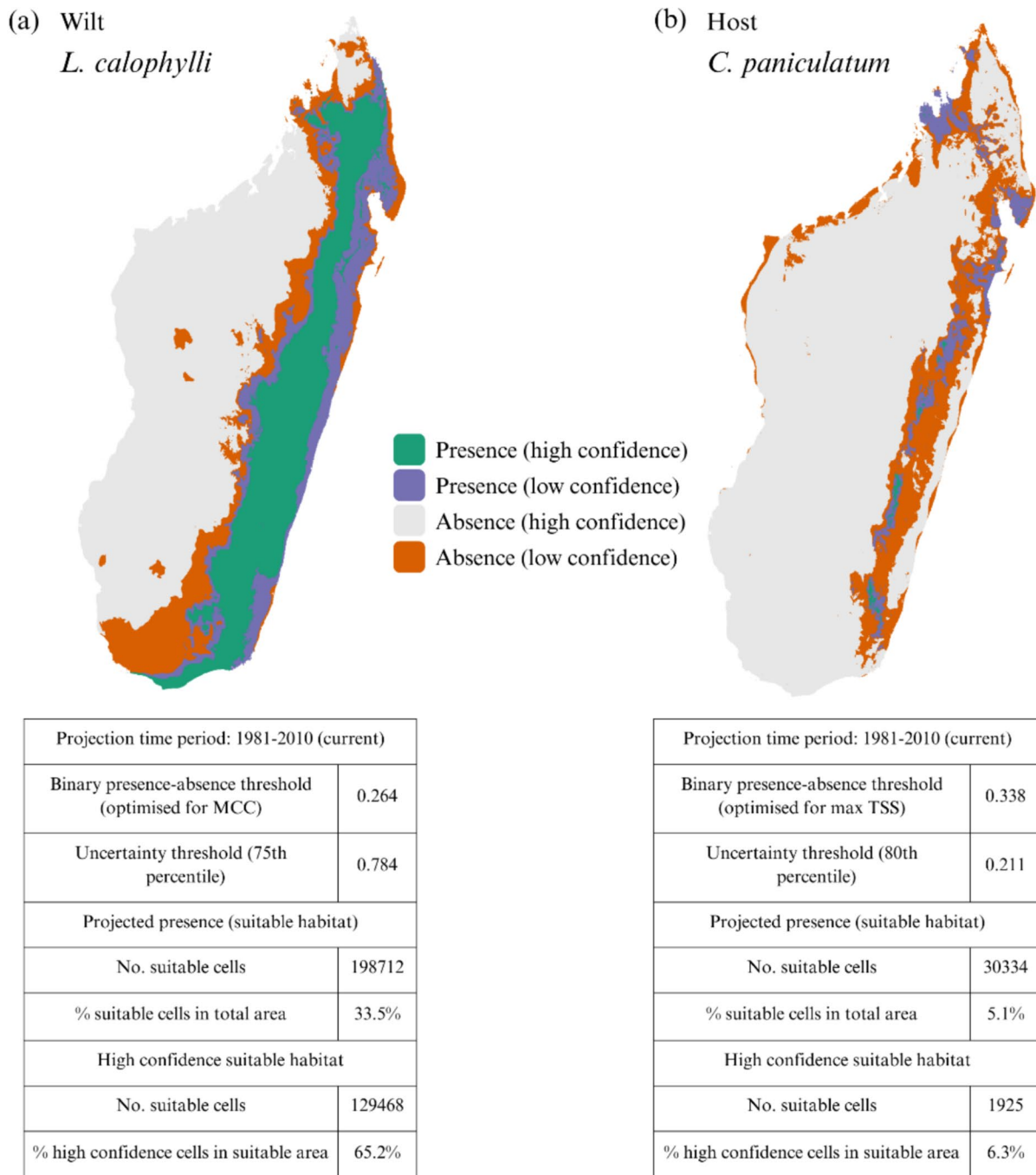


Fig. 2 Current projected binary presence-absence of (a) fungal wilt of *L. calophylli* and (b) *C. paniculatum* with associated confidence categories. Confidence was determined through inverting and thresholding each ensemble model's entropy layer). Green areas on the maps represent high confidence of species presence (where more than 75% of model outputs

agree), and purple areas represent lower confidence presences (less than 25% model outputs agree). With the same method, grey areas on the maps represent high confidence absences, and red shows low confidence absences. For the host tree, mapping prediction uncertainty was calculated using the 80th percentile (as 75th led to zero)

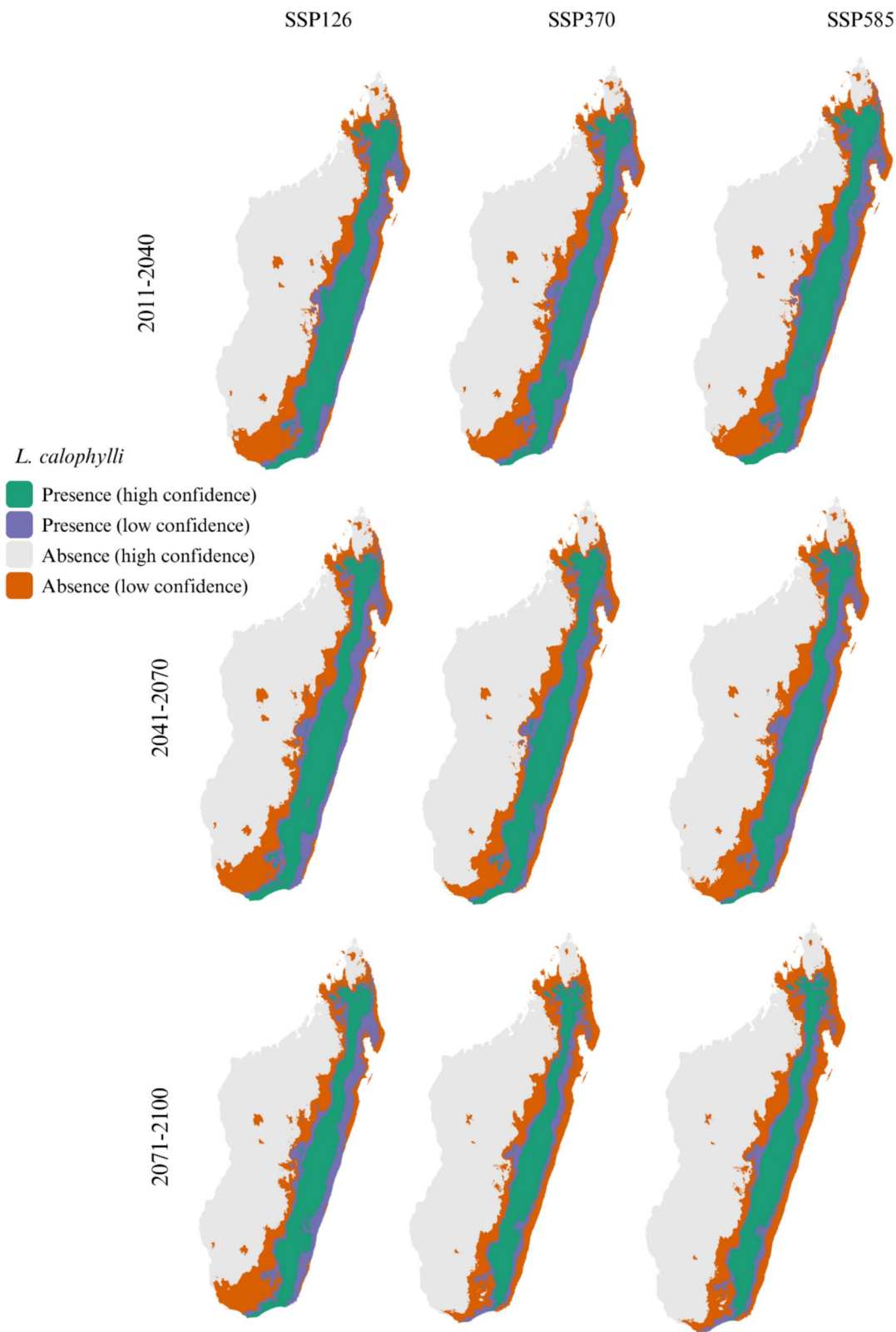


Fig. 3 Future predictions of wilt pathogen *L. calophylli* binary presence-absence across climate scenarios (columns: SSP126, SSP370 and SSP585) and time periods (rows: 2011–2040, 2041–2070, and 2071–2100). Data were converted to binary presence-absence using the ‘minimum distance to ROC curve’ optimisation method in the *sdm* R package. Each binary prediction visualises high and low confidence for presences and absences, using an uncertainty threshold (high confidence where 75% models in ensemble are in agreement). Green areas on the maps represent high confidence species presence, and purple areas represent low confidence presences. Grey areas on the maps represent high confidence absences, and red shows low confidence absences

small patches of uncertainty (low confidence absence – red) around the outside of the projected distribution for the wilt, and in the south and west which does not overlap with the host (Fig. 2a). The host presence distribution is small and isolated, with low confidence absences projected along western coastal fringes.

Spatial–temporal patterns of future range dynamics

Overall, ensemble SDMs for both species project changes in the geographic distributions of suitable habitat of the fungal wilt *L. calophylli*, and endemic host, *C. paniculatum* across all climate scenarios examined. These projections, however, reveal markedly different trajectories for the pathogen and its host, suggesting potential disruption of their current spatial relationship by the end of the century. The wilt pathogen *L. calophylli*, demonstrates considerably greater resilience under future climates, with projected range contractions of only 7.7–31.6% across all scenarios and timeframes (Fig. 3, Online Resource 4, Table S5). Even under the most extreme climate scenario (SSP5) by 2071–2100, the pathogen is projected to retain 68.5% of its current range.

In contrast to the wilt pathogen, *C. paniculatum* is projected to experience severe range shifting, with an overall net contraction across all scenarios, except for the first period (2011–2040 for the low-emission pathway only) (Fig. 4). Moderate reductions of 22.5–41.1% under the low emissions pathway become progressively more severe under higher emission scenarios, with the most extreme reductions of 65.9% by the end of the century observed under the fossil-fuelled shared socioeconomic pathway (Fig. 5, Online Resource 4, Table S5).

Measuring range differences along a temporal gradient reveals distinctly different trajectories of range stability, contraction and expansion. The fungal pathogen shows consistent range stability across scenarios and time periods, with slight expansion into new range by 2040 under high emissions scenario, and even minor expansion by end of century under low emissions scenario (Fig. 5). Meanwhile, a progressive intensification of range contractions across all scenarios (except the low-emissions pathway) are predicted for the host *C. paniculatum*, with the most dramatic changes occurring in the latter half of the century, equating to more than double range losses compared to the wilt (Fig. 5). Towards the end of the century (2071–2100), the most dramatic changes occur, particularly for *C. paniculatum*, which predicts the highest contractions of original range area, along with the lowest levels of stability and expansion compared to earlier in the century. Equally, the pathogen—although still experiencing some range contractions during this period (8.3–31.5%)—maintains relatively high range stability (68.5–91.7%) (Fig. 5, Online Resource 4, Table S5).

L. calophylli exhibits conservative spatial shifts with a consistent directional pattern (Fig. 6, purple icons). These directional shift results reveal a potential spatial decoupling in the geographic responses of host and pathogen. For *C. paniculatum*, predominant shifts were observed in southward and eastward directions across most scenarios, with substantial centroid shifts ranging from 29.7–111.2 km (Fig. 6, green icons). *C. paniculatum* is also predicted to move upslope in the next century, showing a mean elevational increase of 85 m by 2100 (Fig. 7). This directional divergence, with species boundaries moving in different cardinal directions at significantly different rates, suggests potential disruption of their current spatial relationship under future climate scenarios, particularly under high emission pathways and later time periods.

Host–pathogen elevational relationship

Elevation responses show some consistency between host and pathogen (Fig. 7), with both species generally shifting upward in elevation at different rates and thresholds for the focal tree. *C. paniculatum* shows

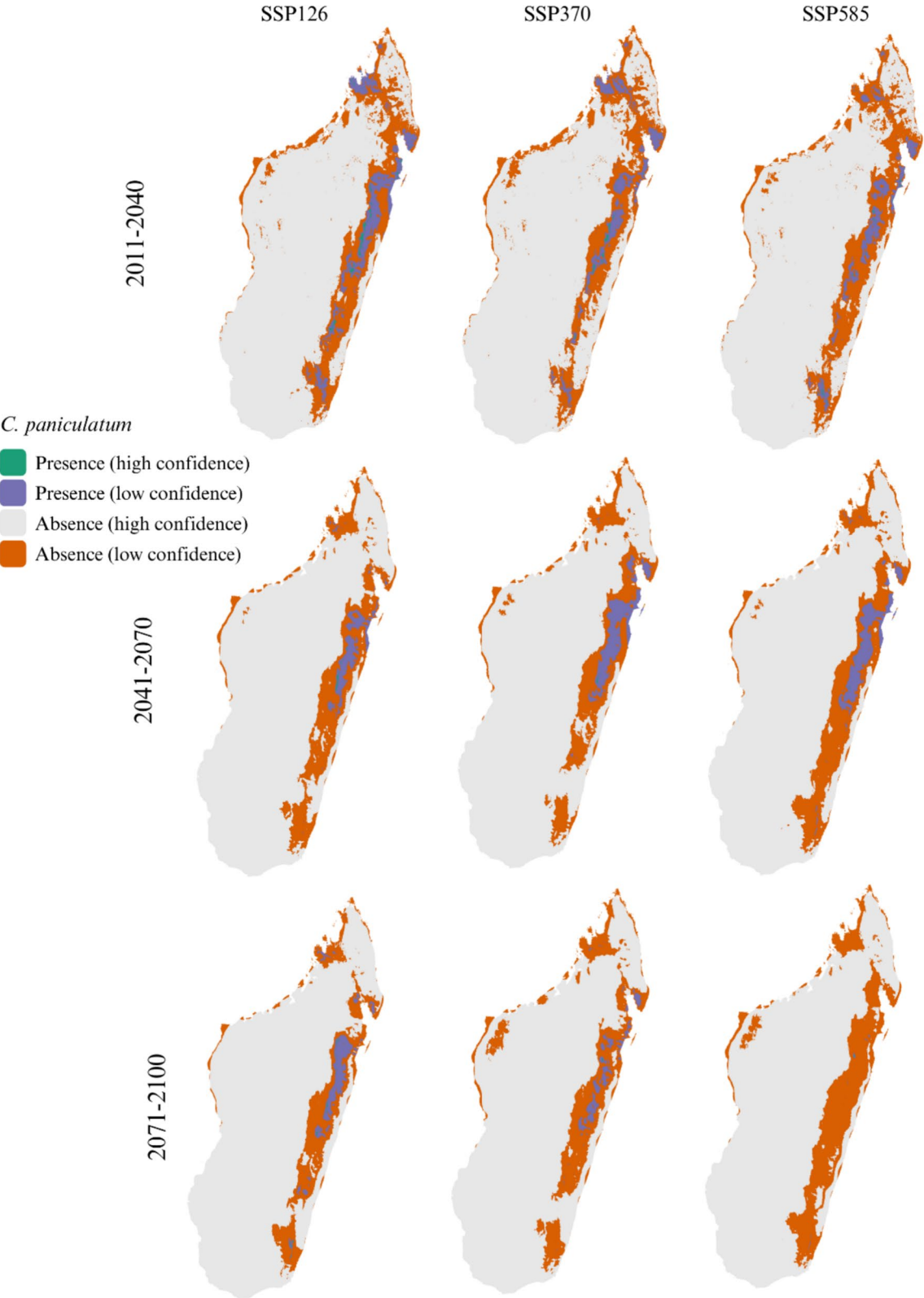


Fig. 4 Future predictions of host *C. paniculatum* binary presence-absence across climate scenarios (columns: SSP126, SSP370 and SSP585) and time periods (rows: 2011–2040, 2041–2070, and 2071–2100). Data were converted to binary presence-absence using the ‘maximising sensitivity and specificity’ optimisation method in the *sdm* R package. Each binary prediction visualises high and low confidence for presences and absences, using an uncertainty threshold (high confidence result is where 80% models in ensemble are in agreement). Green areas on the maps represent high confidence species presence, and purple areas represent low confidence presences. Grey areas on the maps represent high confidence absences, and red shows low confidence absences

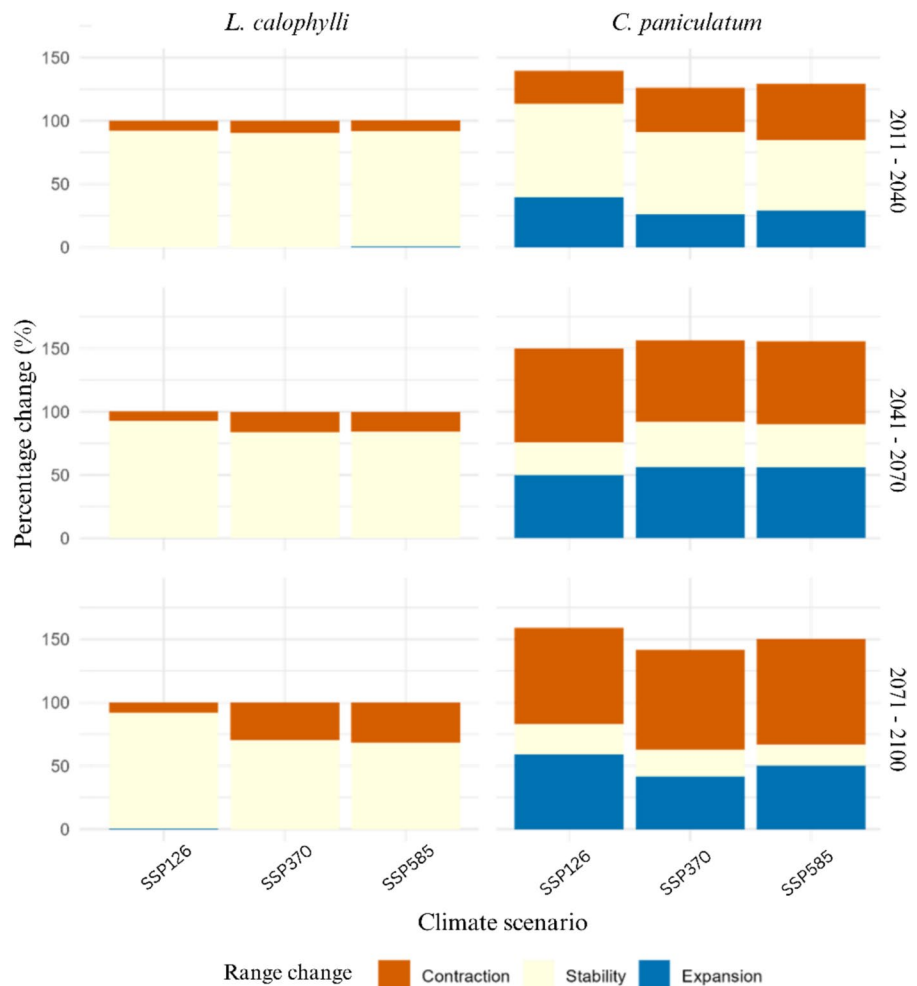
more pronounced elevational shifts (maximum vertical shift height of 253.6 m during 2071–2100 with SSP3) than the pathogen (up to 124.0 m for the SSP5 scenario). These different rates of elevational migration could temporarily alter disease dynamics along

elevation gradients, although given their geographic distributions, the predicted probability of presence of the pathogen exceeds the overall elevational range of *C. paniculatum*.

Geographic range overlap

The predicted distribution of *L. calophylli* dominates the eastern forest corridor, maintaining stable geographic distribution into the future (Figs. 8–9). In contrast, the host, *C. paniculatum*, has a very limited predicted distribution across Madagascar, persisting in patches in the north and isolated locations on the eastern humid belt under future climate and land cover scenarios (Fig. 9). Distribution and overlap changes demonstrate the increasingly limited

Fig. 5 Cumulative range change comparison including predicted percentage contraction (orange – percentage of current range becoming unsuitable in under future climates), stability (light yellow – proportion of current range that is maintained) and expansion (blue – proportion of future range that is newly suitable) for *L. calophylli* and *C. paniculatum* by climate scenario (SSP126, SSP370, SSP585) and time frame (2011–2040, 2041–2070, 2071–2100). Percentages are higher than 100% as the bars are stacked and proportional change to both current (contraction and stability) and future (expansion)



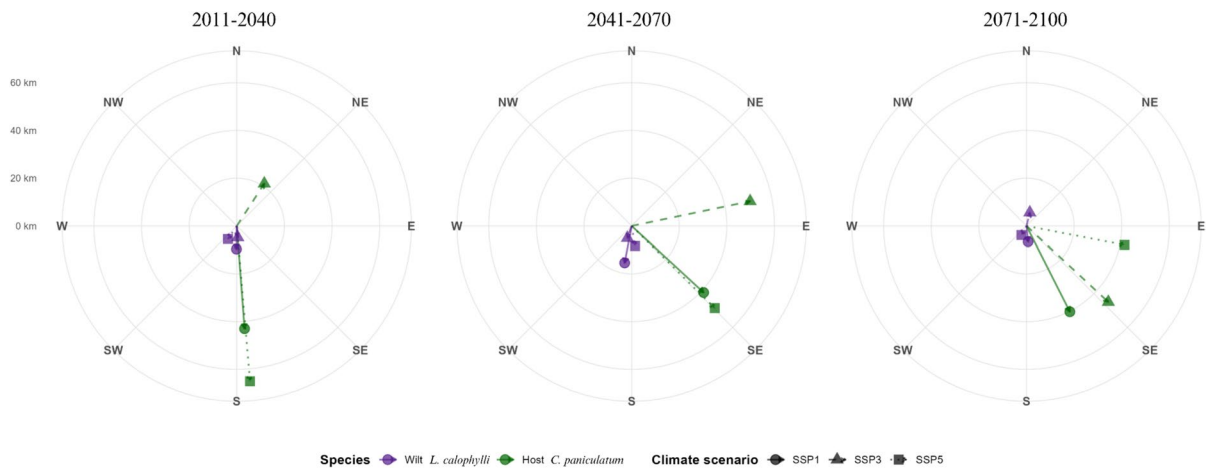


Fig. 6 Centroid shift direction (cardinal and ordinal) and magnitude (km) shown for wilt pathogen (*L. calophylli* – purple) and host (*C. paniculatum* – green) across three future time frames and future climate scenarios (low-emissions (SSP1) –

circle, medium scenario of high-emissions regional rivalry (SSP3) – triangle, high emissions fossil fuelled scenario (SSP5) – square

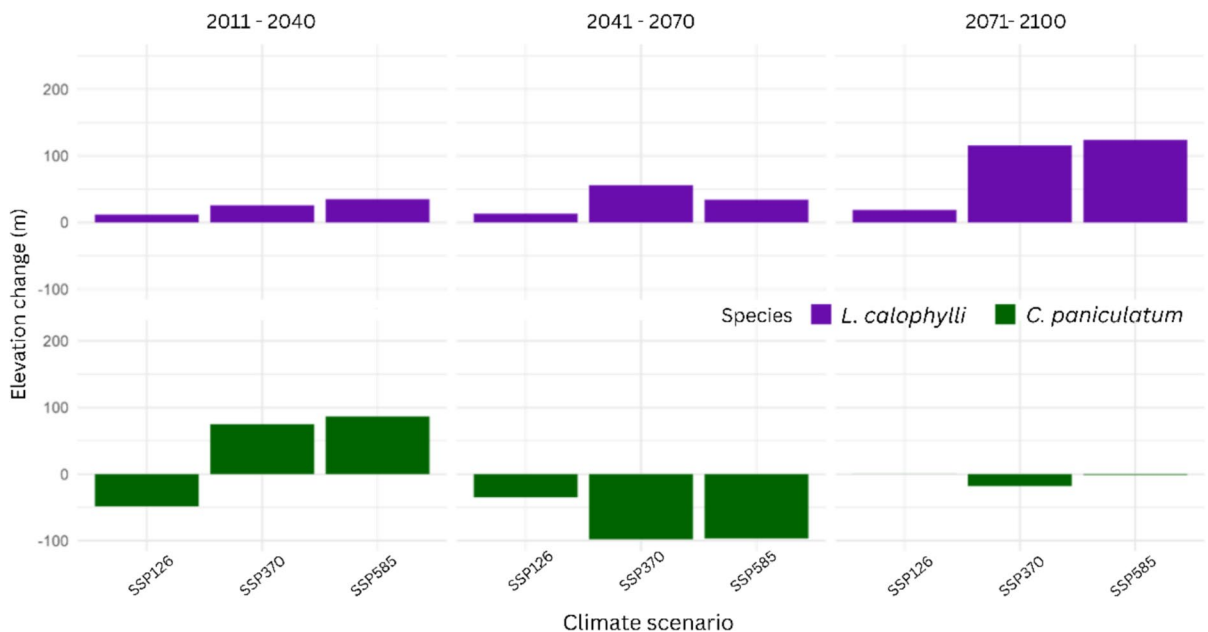


Fig. 7 Predicted elevational range shifts by species, year and scenario between 2010 and 2100. The top row shows wilt pathogen *L. calophylli* (purple), converted to binary presence using the ‘minimum distance to ROC curve’ optimisation threshold. The bottom row shows *C. paniculatum* elevational

range changes (green) using the ‘maximising the sum of sensitivity and specificity’ threshold. Climate scenarios represent low-emissions, sustainable pathway (SSP1), high-emissions regional rivalry (SSP3) and high-emissions, fossil-fuelled pathway (SSP5)

distribution of *C. paniculatum* along the northern and central eastern zones, while for the wilt *L. calophylli*, a pattern of expanding distribution along

Madagascar’s humid forest corridor. Their areas of potential overlap are concentrated along the central-eastern forests, particularly in the north (Fig. 9).

Fig. 8 Future predicted distributions of *L. calophylli* (purple) and *C. paniculatum* (green), and their combined overlap (black) for each future year-range (columns) and climate scenario (rows). These distributions have been created using a binary threshold optimisation, maximising Sum of Sensitivity and Specificity for *C. paniculatum* and the Minimum Distance to ROC Curve for *L. calophylli* (Online Resource 4, Table S4)

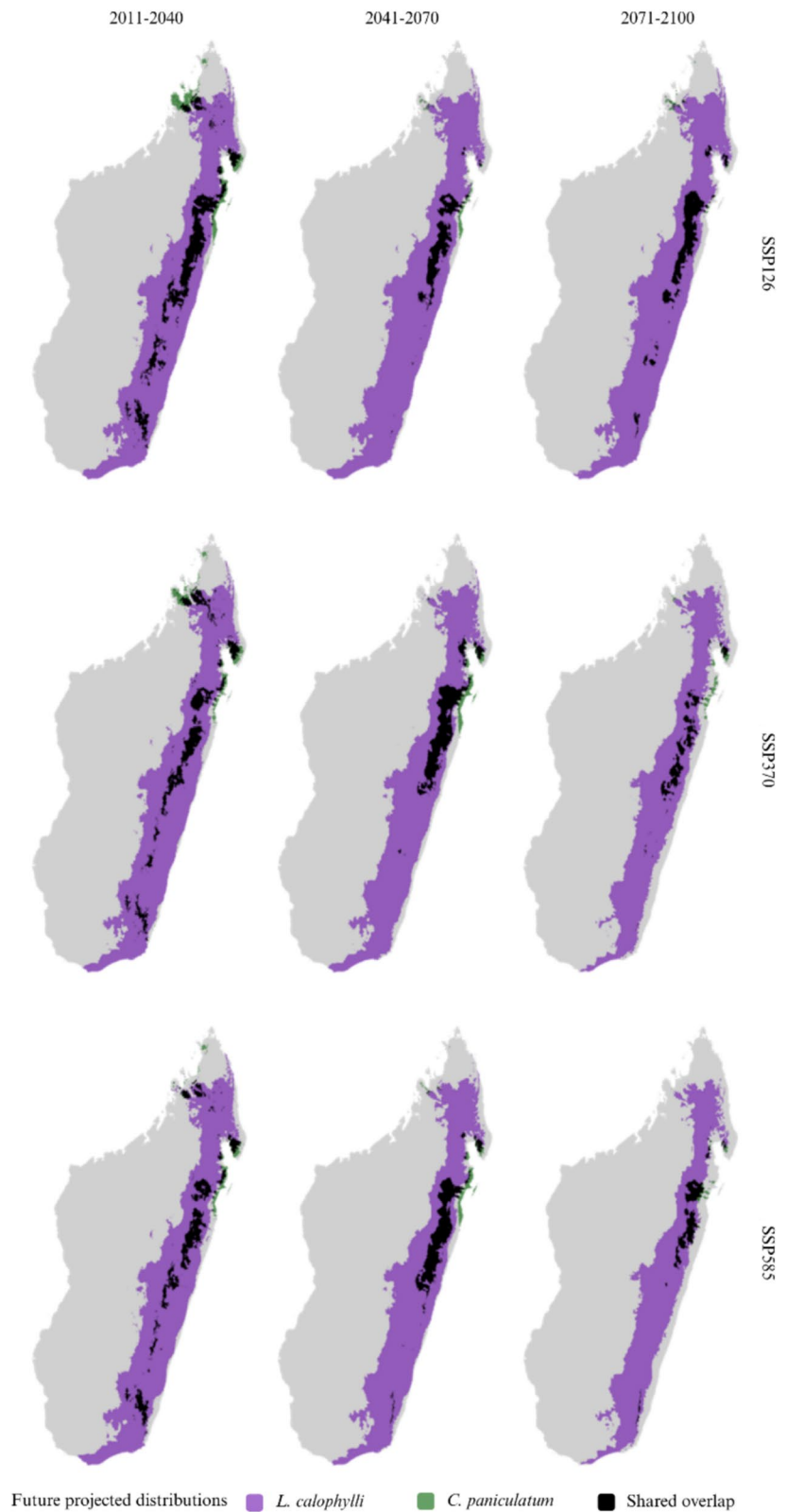
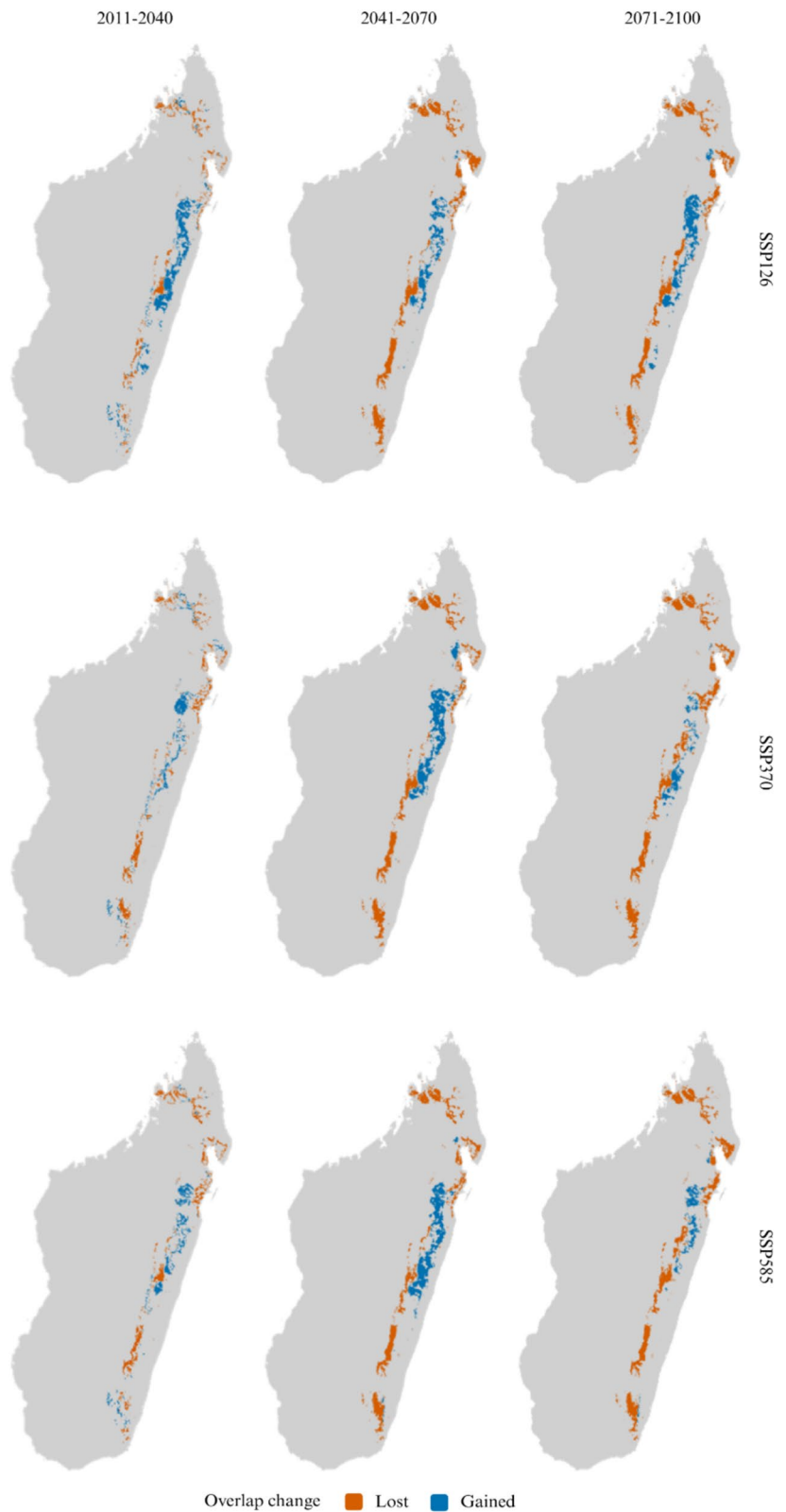


Fig. 9 Future predicted cumulative spatial overlap gain (blue) and loss (orange) between the fungal wilt pathogen (*L. calophylli*) and host tree (*C. paniculatum*) and for each future year-range (columns) and future climate scenario (rows). The underlying predicted distributions in which the overlap was calculated were created using a binary threshold optimisation, Maximising the Sum of Sensitivity and Specificity (opt 2) for *C. paniculatum*, and the Minimum Distance to ROC Curve (opt 4) for *L. calophylli* (Online Resource 4, Table S4). Each overlapping cell change is measured between the current projection and the respective future year



Across all climate and land cover pathways, there is a clear geographic stability of *L. calophylli* to 2100, with the low-emission fossil fuelled pathway showing the most extensive geographic distribution of the pathogen by the late century. Their predicted, shared overlap reduces over time, both by shared pathway intensity and future year range, likely due to the overall contraction in the range of *C. paniculatum* (Fig. 8). The overlap change patterns suggest a southward shift in overlap areas over time.

Standardised range shift metrics (habitat exposure and predicted area of occupancy) show *C. paniculatum* to be much more vulnerable to future change drivers than the wilt pathogen *L. calophylli*. Both show increasing vulnerability as the intensity of future climate scenario increases from 1 (low emissions) to 5 (high emissions), but *C. paniculatum* shows steeper declines and more variability of results across scenarios (Table 1). *C. paniculatum* exhibits high habitat exposure values (0.759–0.830), particularly under higher emission scenarios, indicating widespread habitat transformation to new areas by 2100. Climate exposure is lower for the wilt pathogen *L. calophylli*, and lowest (0.083) under the low-emission pathway (SSP1) but increases substantially under higher emission scenarios (0.298–0.315). The

difference in habitat exposure between species suggests substantially greater climate sensitivity for the host tree. Potential area of occupancy (pAOO) changes show on average, that *C. paniculatum* is forecasted to lose up to 67% of its current area by 2100, compared to *L. calophylli*, which is a much lower predicted loss at up to 31% (Table 1).

Discussion

Environmental change expands invasion opportunity in Madagascar

This study has three key findings that together clarify how global environmental change can reshape host–pathogen dynamics and invasion processes in tropical biodiversity hotspots. First, future climate change consistently maintains or expands climatically suitable habitat for the novel pathogen *L. calophylli* across much of Madagascar, even under high-emissions scenarios. Second, the endemic host *C. paniculatum* is projected to undergo consistent range contraction across all climate scenarios, compounded by fragmentation and dispersal limitation from deforestation, resulting in a small number of geographically isolated refugia by late century. Third, these contrasting responses generate a pronounced spatial and climatic decoupling between host and pathogen distributions, such that pathogen suitability increasingly exceeds and spatially envelops the shrinking host range. Similar host–pathogen climatic mismatches have been documented historically in temperate regions following introduction of invasive pathogens under changing environmental conditions, most notably the extirpation of American chestnut (*Castanea dentata*) by the introduced fungus *Cryphonectria parasitica* (Anagnostakis 1987; Santini et al. 2013) and the widespread collapse of elm populations following invasion of Dutch elm disease (*Ophiostoma spp*) (Karnosky 1979; Santini et al. 2013). In those invasions, pathogen persistence and geographic spread far exceeded the demographic and climatic resilience of their primary hosts, restructuring forest composition for decades to centuries (Santini et al. 2013). Our projections suggest that *L. calophylli* may follow a comparable trajectory in Madagascar, persisting across landscapes even as the endemic host becomes increasingly rare and spatially fragmented.

Table 1 Standardised range shift metrics—habitat exposure index and potential area of occupancy (pAOO) change for each species and emissions scenario compared between current projections and year 2100

Model	Climate pathway*	Habitat exposure index**	IUCN pAOO % change**
Wilt pathogen <i>L. calophylli</i>	SSP1	0.083	−7.936
	SSP3	0.298	−28.986
	SSP5	0.315	−30.656
Host <i>C. paniculatum</i>	SSP1	0.759	−45.173
	SSP3	0.786	−64.047
	SSP5	0.830	−67.485

*SSP1=low-emissions, sustainable socio-economic scenario; SSP3=high emissions, regional rivalry scenario; SSP5=high emissions, fossil-fuelled scenario

**Range shift metrics (habitat exposure and pAOO) were computed after converting continuous probability of presence to binary presence-absence predictions. We used species specific binary optimisation thresholds: *L. calophylli* models were optimised for the minimum distance to ROC curve. Host plant model optimised for maximizing the sum of sensitivity and specificity (TSS)

The projected stability and breadth of the climatic niche of *L. calophylli* indicate that the pathogen is unlikely to be constrained by future climate change in the same way its host is. Under high-emission scenarios, orders of magnitude more areas are predicted to be climatically suitable for the pathogen by the end of the century, compared to *C. paniculatum*. *L. calophylli* may, consequently, remain in local forests regardless of whether *C. paniculatum* becomes locally extirpated across its range, increasing the likelihood of spill over into other native species or reinfection of remnant populations. This depends on whether the pathogen is host-specific or not. It has been observed in other forest pathogens that multi-host strategies allow pathogens to maintain populations in a reservoir host even as susceptible species decline (Desprez-Loustau et al. 2007), but whether this occurs in Madagascar remains a future research area to explore.

By maintaining the area of climatically suitable habitat for *L. calophylli*, climate change effectively increases the invasion opportunity available to this novel pathogen. Here, *invasion opportunity* refers to the total extent of environments in which establishment and long-term persistence are climatically plausible. As suitable landscape increases, the probability that repeated introduction events result in successful establishment also increases, even if the likelihood of establishment per individual introduction remains unchanged. This distinction is critical for forest pathogens, where propagule pressure is typically chronic rather than episodic (Garbelotto and Pautasso 2012; Lovett et al. 2016). For instance, continued movement of timber or contaminated equipment can generate multiple introduction events over time, and a larger suitable area increases the chance that at least some of these introductions occur in environments conducive to persistence (Santini et al. 2013). Alternatively, if climate change reduces suitable habitat for *L. calophylli*, repeated introductions would more often fail because arrival events would disproportionately occur in environmentally mismatched locations (Meentemeyer et al. 2011). However, our projections suggest the opposite trajectory. By expanding or maintaining climatic suitability across large parts of the island, environmental change weakens climatic barriers to establishment and makes invasion outcomes increasingly dependent on propagule pressure rather than environmental mismatch. In this way, climate

change increases invasion opportunity and the likelihood that repeated introductions translate into establishment (Elad and Pertot 2014), causing early mortality to already climatically weakened hosts like *C. paniculatum*.

Importantly, the asymmetry of future habitat suitability between host and pathogen highlighted in this study is supported by multiple, independent diagnostics rather than being an artefact of model transfer or threshold choice. The MESS analysis (Online Resource 4, Figure S14) indicated that future projections for *L. calophylli* are made within environmental space represented by the training data, reducing the likelihood that the observed broad pathogen suitability arises from extrapolation into novel climates. Additionally, uncertainty mapping shows persistent areas of high model agreement for the pathogen across Madagascar's humid forests. Together, these diagnostics strengthen confidence that the projected divergence reflects a real difference in (pathogen) climatic tolerance and (host) vulnerability, rather than modelling artefacts. Notwithstanding, the predicted distributions represent fully realised climatic suitability rather than realised occupancy and therefore cannot be interpreted as direct predictions of current spread or disease extent.

Management implications and future conservation directions

The contrasting responses the wilt pathogen *L. calophylli* to the endemic host tree *C. paniculatum* depict a troubling dimension to potential climate change impacts that extends beyond species range shifts. While the host faces clear range contractions, the pathogen shows steady tolerance to changes in the climate over time, with minor projected range losses across the same scenarios and time frames. This disparity creates an ecological mismatch that has concerning implications for forest health and conservation planning. In the current-day projected distribution of *L. calophylli*, the geographical range of presence spans a broader climate niche, extending much further longitudinally, with reducing but visible presence stretching from sea-level at the eastern coastline all the way westward, through the humid into the sub-humid region, and even into drier savanna land towards the centre of the country. This

broader distribution suggests the pathogen can persist under climate conditions that far exceed the physiological limits of *C. paniculatum*. *L. calophylli* maintains suitable habitat in most of Madagascar's central spine and eastern escarpment, covering most of the humid zone, and parts of the eastern sub-humid zone. This suggests that the pathogen could survive as a generalist and not require *C. paniculatum* specifically as a host for survival, where it may utilise other species as a 'reservoir' in areas where their ranges do intersect (Grünwald et al. 2008; Rizzo and Garbelotto 2003).

In addition, the wilt pathogen *L. calophylli* causing mortality of *C. paniculatum* in Madagascar and *C. inophyllum* on nearby tropical islands is still an unknown to the conservation community. In the face of becoming widespread before official identification, our study provides a timely assessment of the potential impacts of *L. calophylli* on a focal endemic tree species in a tropical biodiversity hotspot. We provide suggestions for how predictive ecological modelling can support wider efforts to identify, monitor, and limit its spread by recommending that future work focuses on the following research questions and actions:

1. Host range and other targets

Research question: Do we know with certainty, that *L. calophylli* does not also infect or impact other endemic species or genera in Madagascar?

- **Action:** Collaborate with local partners to conduct systematic field sampling of multiple species across sites within the core probability of presence distributions of *L. calophylli*.
- **Action:** Collaborate with pathologists to officially identify the pathogen.

2. Phase of spread

Research question: What phase of spread is the pathogen in?

- **Action:** random sampling of species and sites within and *outside* of the probability of presence distribution of *L. calophylli*.
- **Action:** Multi-criteria analysis (MCA) to map the possible spread start point and dispersal patterns, using anthropogenic and

natural spread routes: ferry ports, roads, known logging areas, built-up areas, hiking paths, prevailing wind direction and river catchments.

3. Application of global tools

Research question: How can IPBES tools and suggestions for invasive species management (IPBES 2023) be adapted to the case of *L. calophylli* in the context of tropical, island biodiversity?

- **Action:** Assess applicability of IPBES frameworks (IPBES 2023) for prevention, early detection and rapid response in Madagascar's ecological and policy context.

Limitations and assumptions

Our study is underpinned by important assumptions and limitations that warrant consideration when interpreting and drawing conclusions from SDMs. First, models are built on all available, yet a limited number of occurrence records. To avoid overfitting, we adhered to the recommended ratio of 8–10 occurrences per predictor (Guisan and Zimmermann 2000; Merow et al. 2013) during model construction. This can lead to oversimplification of complex ecological processes and could overestimate the predicted range of the fungal pathogen. Notwithstanding, overestimation is preferential when little is known of pathogen spread, virulence or potential socioeconomic costs. Second, as with most correlative SDM frameworks, our approach assumes that species are in equilibrium with current climatic conditions and occupy all areas that are environmentally suitable. However, observed distributions are often constrained by dispersal limitation, topographic barriers and disequilibrium resulting from past climate change (Svenning and Sandel 2013). This issue may be particularly important for predictions of *L. calophylli*, because the occurrence data were extracted at the genus level and combined records from multiple species that may have distinct environmental tolerances. Third, SDM frameworks are inherently better suited to modelling the realised niche than the fundamental niche (Soberón, 2005). As a result, our models describe the environmental conditions under which the pathogen is currently

found, rather than the full range of conditions it could potentially tolerate. Although the host tree may be capable of persisting under a broader range of environmental conditions than those represented in the available records, we used all confirmed occurrence records from the pathogen's endemic range in Madagascar. This helps reduce the risk of niche truncation and increases confidence that the models capture the pathogen's realised environment space within its native distribution.

Finally, when transferring models from mainland Africa to Madagascar, we acknowledge the uncertainty associated with extrapolating into novel environmental conditions (Elith et al. 2010). However, our Multivariate Environmental Similarity Surface (MESS) analysis indicated that novel conditions were minimal for both the endemic Malagasy host (<0.6%) and the extrapolated fungal pathogen (nearly 0%). This suggests a high degree of environmental similarity between the training and projection regions, increasing confidence in model transferability (Elith et al. 2010; Owens et al. 2013).

Conclusion

We highlight that the range dynamics of a non-native, incipient pathogen can become a bigger threat to endemic island species under climate change. We identified and compared the current and future predicted geographic distributions of the wilt pathogen *L. calophylli* in relation to those of host *C. paniculatum*, and quantified predicted range changes and potential future spatial overlap. We showed the already sparse, currently suitable habitat of *C. paniculatum* may reduce further to isolated fragments in the central and north sub-humid ecoregions, as a direct result of combined climate change and deforestation by the end of this century. On the other hand, the climate resilience shown by the fungal wilt pathogen *L. calophylli*, across all measured climate projections, without a strong reliance on forested areas for survival could further put endemic vulnerable host species at risk. These findings should alert the conservation community to explore the impacts of multiple global and regional change drivers simultaneously for other vulnerable and endangered species across the tropics, to better understand current future threats to

species' survival, and to limit further biodiversity loss across terrestrial biodiversity hotspots globally.

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Data Availability All data used in this study are derived from publicly available repositories and referenced in the manuscript accordingly: Global portals: GBIF, CHELSA, ForestAtRisk. Publicly available survey data from published peer-reviewed articles: Ramananjato, V., Razafindratsima, Onja. 2021. Data from: Structure of microhabitats used by *Microcebus rufus* across a heterogeneous landscape [Dataset]. <https://doi.org/10.5061/dryad.2280gb5rs>. Armstrong, A. H., Shugart, H. H. & Fatoyinbo, T. E. 2011. Characterization of Community Composition and Forest Structure in a Madagascar Lowland Rainforest. *Tropical Conservation Science*, 4, 428-444. <https://doi.org/10.1177/194008291100400406>. Wright, P. C., Otero Jimenez, B., Rakotonirina, P., Andriananoely, D. H., Shea, A., Ratalata, B. & Razafimahaimodison, J. C. 2020. The Progressive Spread of the Vascular Wilt Like Pathogen of *Calophyllum* Detected in Ranomafana National Park, Madagascar. *Frontiers in Forests and Global Change*. <https://doi.org/10.3389/ffgc.2020.00091>. All custom code used for all preparation and analyses can be found at: <https://github.com/GeoEmma/Underwood-fungal-host-SDMs-2026>.

Declarations

Competing Interests The authors declare no competing interests.

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