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Predicting habitat suitability for the Australian cycad-attacking weevil (*Siraton internatus*) under climate change

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Abstract Cycads hold important economic and conservation value. Some species are extensively used in landscaping, while others are endangered and legally protected. The Australian cycad-attacking weevil, *Siraton internatus*, is notably destructive, occasionally causing infestations and invasions across various countries. This study simulated habitat suitability for *S. internatus* to assess its potential invasion and the impact of climate change. Habitat suitability was evaluated under current climate and four climate change scenarios over two time frames (2050 and 2090). Furthermore, we investigated the threat posed by *S. internatus* to cycad reserves, using Taiwanese reserves as a representative case. Our MaxEnt predictions demonstrated high accuracy, meeting multiple evaluation criteria. We explored the potential distribution of *S. internatus* within Australia and internationally, identifying suitable habitats in Africa, the Americas, Asia, and Europe. The case study highlighted the low habitat suitability within the two Taiwanese cycad reserves, which is projected to decrease to unsuitable levels under future climate change scenarios for this weevil species. Moreover, our results revealed that suitable habitat for *S. internatus* is projected to contract globally under all climate scenarios and time periods, but expansion in Chile and the southern Himalaya (e.g., Nepal). This study provides valuable insights into cycad conservation and pest invasion risks. The results support both global and local efforts to manage the invasion threats from this destructive Australian cycad-attacking weevil species. It also accentuates the urgency for continuous biosecurity inspections and prevention of exporting mature cycad caudexes from Australia.

Keywords Distribution modeling · Cycad conservation · Global warming · Invasion · Future climate scenarios

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Introduction

Cycads (Cycadales) are ancient gymnosperms with perennial woody structures that resemble palm trees. Notably diverse and widespread during the Mesozoic, cycads have evolved with minimal morphological variation, earning them the nickname "living fossils". Despite their well-documented toxicity, cycads have played an important role in human culture and have economic value (Whiting 1963; Kobayashi et al. 1974; Whitelock 2002; Hayward and Kuwahara 2012). *Cycas revoluta*, for instance, is a preferred choice in horticulture, frequently found in bonsai gardens and parks (Lu 2004; Tan and Ji 2010). However, not all cycads enjoy such widespread cultivation. A majority of identified cycad species are on the IUCN Red List of Threatened Species (IUCN 2023), highlighting their conservation vulnerability. Many are also protected under the Appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and have national reserves dedicated to their protection. In Taiwan, for instance, the Coastal Range Taitung Cycas Forest Reserve (CMR) and Hongye Village Taitung Cycas Nature Reserve (HCR) are specifically designated for the protection of the endemic *Cy. taitungensis* (Fig. S1), underscoring the targeted efforts to conserve this unique species, alongside others like *Cy. panzhihuaensis* in China and *Encephalarto slatifrons* and *E. latifrons* in South Africa.

Nevertheless, despite stringent international and local legislative protections, cycads face grave challenges (IUCN 2023). The Anthropocene era has seen an escalation in human activities, such as deforestation for agricultural expansion and urban development, leading to significant losses in cycad habitats. These ancient plants also suffer from the horticultural appeal that makes rare species targets for illegal poaching and trading, further endangering their existence. Invasive pests, such as the cycad blue butterfly *Chilades pandava* and the scale insect *Aulacaspis yasumatsui*, pose additional threats, weakening the plants and making them more susceptible to diseases (Takagi 1977; Chang 1989). Climate change compounds these issues, potentially altering ecological niches and enabling more frequent biological invasions (Nogué et al. 2009; Swart et al. 2018; Naimi et al. 2022). Given these multifaceted threats, prioritizing cycad conservation is imperative. This requires strengthening legal protections, enhancing international cooperation, involving local communities, and advancing scientific research to safeguard these essential elements of global biodiversity.

Trunk-boring cycad weevils, particularly *Siraton internatus* (may be transferred to the genus *Demyrsus* Pascoe, 1872 based on the recent phylogenetic study of Hsiao et al. (2023)), pose a major threat to cycads, and prefering stressed, diseased, or dying plants (Fig. 1) (Oberprieler 1995; Tang and Oberprieler 2006). While *S. internatus* naturally occur in low densities and primarily feeds on *Macrozamia* cycads in native coastal areas from New South Wales to Queensland, it has infested various cycad genera in artificial environments, including *Macrozamia*, *Lepidozamia*, *Encephalartos*, *Zamia*, and *Cycas* species (Glass 1980; Kennedy 1992, 2011; Oberprieler and Caldara 2012). Its damaging potential is evident in botanical gardens and nurseries, where both seedlings and mature plants are vulnerable (Westwood 1886; Glass 1980; Kennedy 1992, 2011; Oberprieler and Caldara 2012). For example, extensive infestations of *S. internatus* causing the death of *Encephalartos* plants and a 30-year-old *Zamia furfuracea* (Kennedy 1992, 2011). Managing *S. internatus* is challenging due to its deep burrowing nature, which shields it from traditional control methods. In addition, its unintentional introduction to various global regions has been documented over the past 130 years, underscoring its invasive nature (Glass 1980; Kennedy 1992, 2011), including Belgium (Westwood 1886), Italy, Greece (Hustache 1934), USA (California) (Glass 1980; Kennedy 1992, 2011; Oberprieler and Caldara 2012; INVASIVE.ORG 2023). These historical records serve as a reminder that weevils have the potential to invade and negatively impact cycad populations worldwide, highlighting the ongoing threat they pose. However, the scarcity of detailed biological knowledge on *S. internatus* hampers effective control and management strategies.

This study aims to address the knowledge gap regarding the potential invasion and climate change response of *S. internatus* by accessing its potential distribution under present and future climate scenarios. We focused on evaluating the threat to national cycad reserves through a detailed case study (CMR and HCR in Taiwan) (Fig. S1). Our approach included compiling global occurrence of *S. internatus* from museum collections and literature to ensure the data

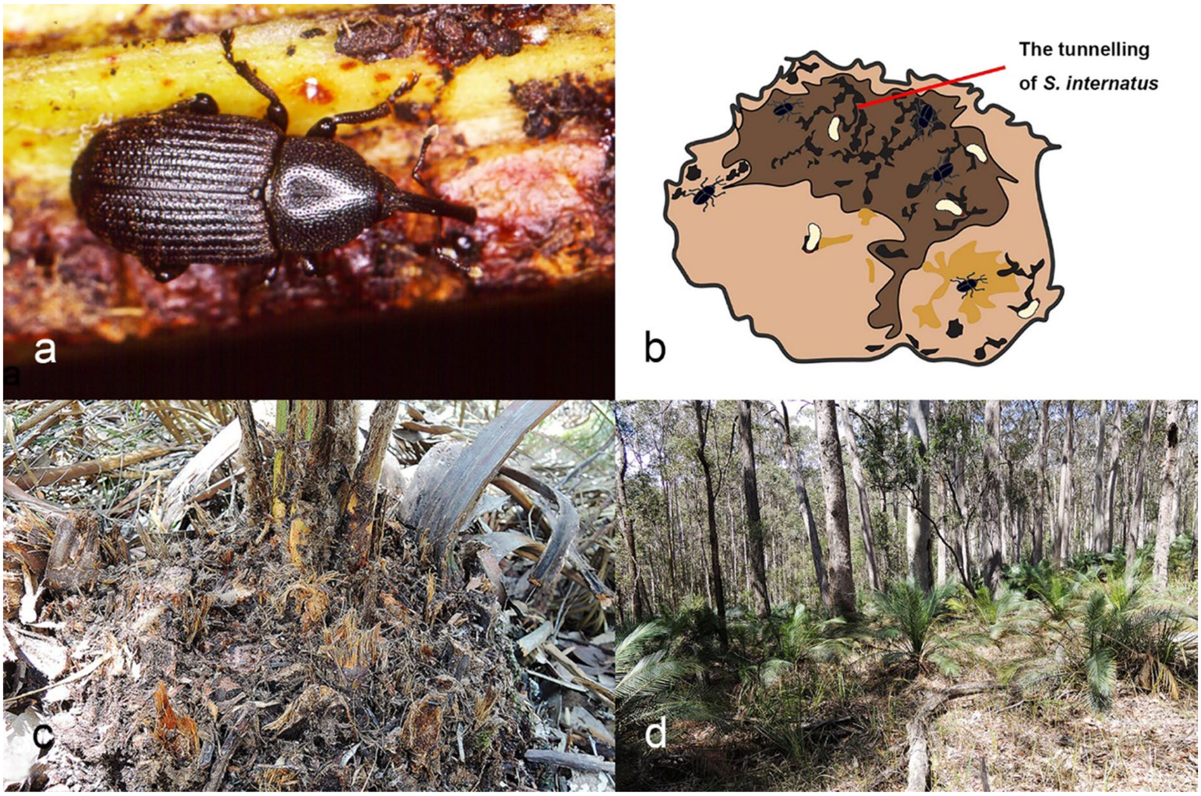

Fig. 1 The infestation of *Siraton internatus* and their natural habitat: **a** adult of *S. internatus*; **b** illustration depicting the infestation of *S. internatus* and the tunneling of their larvae; **c** preference of *S. internatus* for unhealthy and dying cycad plants; **d** natural habitat and host plants (*Macrozamia communis*) of *S. internatus* in New South Wales

accuracy. Secondly, considering the current limitations in comprehensive biological data for *S. internatus*, we utilized MaxEnt for modeling its habitat suitability, relying primarily on climatic variables. This approach enabled us to conduct analyses at global, Australian, and Taiwanese scales, despite the data scarcity in specific biological traits of the species. Finally, we projected future range shift under varied climate change scenarios. This study is intended to enhance our understanding of cycad conservation and weevil invasion management, equipping us with knowledge to devise effective conservation strategies.

Materials and methods

This study investigated the potential distribution of *S. internatus* and its impact under changing climate conditions, proposing recommendations for the conservation of cycads and management of weevil invasions. The research was conducted in three main phases: Firstly, global occurrence data for *S. internatus* were meticulously compiled from reputable sources, including museum collections and peer-reviewed publications, to minimize biases in our model predictions (see 'Species occurrence dataset and bioclimatic factors'). Secondly, we focused on selecting the most suitable variables and optimizing the model parameters for accurate predictions (see 'Variable selection process' and 'Model parameter settings and optimization'). Lastly, we validated the robustness of our models through various metrics and visualized potential distributions on maps to illustrate the impact of different climate scenarios on habitat suitability (see 'Model prediction and map visualization' and 'Model validation').

Species occurrence dataset and bioclimatic factors

Global occurrence data for *S. internatus* were meticulously complied from reputable sources, including museum collections and peer-reviewed publications (Hsiao and Oberprieler 2020, 2021). To ensure the highest data accuracy, each record underwent rigorous verification, including expert taxonomic identification and cross-referencing with established distribution records to minimize biases in our model predictions. Furthermore, Quantum GIS (QGIS 2022) was employed to ensure a single distribution point within each 10-min grid cell, and to eliminate duplicate and imbalanced dataset to avoid severe spatial and environmental bias (Merow et al. 2013). Although this weevil's primary distribution is in Australia, invasions in Europe and North America have been documented (Fig. 2a; Table S1). A comprehensive compilation of 58 *S. internatus* occurrences was organized and stored in a Microsoft Excel spreadsheet. The data were then saved in comma-separated value file format for further analysis and modeling using the MaxEnt software (Phillips et al. 2006). In addition, we kept all data publicly available for future validation as recommended by Liao et al. (2023).

We sourced nineteen bioclimatic variables (1970–2000) related to temperature and precipitation, which influence small arthropods' distribution and survival, were sourced from WorldClim (version 2.1) (Fick and Hijmans 2017). Future projection using the GCM GISS-E2-1-G (Coupled Model Inter-comparison Project Phase VI, CMIP6) under four shared socioeconomic pathway scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5) for 2050 and 2090 timeframes was used in our model to assess the potential impacts of climate change on habitat suitability for *S. internatus*. The GISS-E2-1-G climate model from NASA is renowned for its enhanced climate sensitivity, making it apt for studying future warming pattern (Kelley et al. 2020; Nazarenko et al. 2022). The four socioeconomic pathway scenarios represent contrasting levels of climate change signals, with SSP1-2.6 indicating the optimistic scenario with climate protection measures are being taken and SSP5-8.5 representing the strongest. This multi-decadal time frame allows us to track and observe trends in the distributional shift of *S. internatus* in response to climate change. We obtained data at a 10-min resolution for global analysis and a 30-s resolution for in-depth Australia and Taiwan analyses.

Variable selection process

We prioritized addressing multicollinearity and the ratio of sample size to features, which are critical for maintaining the integrity and predictability of our ecological models. Our initial analysis utilized 19 bioclimatic variables to comprehensively assess each variable's contribution and permutation importance, allowing us to discern their significance within the model. This selection process involved choosing the top five variables based on contribution rates and the top five based on permutation importance. This resulted in a combined list of eight unique variables due to overlap. Subsequently, these variables underwent a Variance Inflation Factor (VIF) analysis to eliminate highly multicollinear features. Following the VIF criteria (Montgomery and Peck 1992; Thompson et al. 2017), we selected three variables with VIF values below the threshold of 10. Additionally, we included bio08, which had a VIF of 13.2, slightly above our primary threshold but considered manageable. After a second round of VIF analysis, we confirmed that the four selected variables—Isothermality (bio03), Precipitation of the Driest Quarter (bio17), Mean Temperature of the Wettest Quarter (bio08), and Precipitation of the Coldest Quarter (bio19)—all exhibited low multicollinearity. These variables, detailed in Table 1, were identified as most predictive of *S. internatus* habitat suitability, ensuring our model was scientifically grounded and reliable.

Model parameter settings and optimization

Given the limited biological information available about *S. internatus*, we utilized MaxEnt for species distribution modeling as it effectively leverages presence-only data, potentially revealing informative distributions before the pest invasion (Yeh et al. 2021; Baradevanal et al. 2023; da Silva et al. 2023). We used MaxEnt version 3.4.4 (Phillips et al. 2023) in R version 4.3.2 (R Core Team 2023) with the RStudio interface (version 2023.09.01+494) (RStudio Team 2023) and the 'dismo' package (Hijmans et al. 2022), to predict the global and Taiwanese distribution of the weevil. Pseudo-absences were generated from presence-only data, with the model configured to select

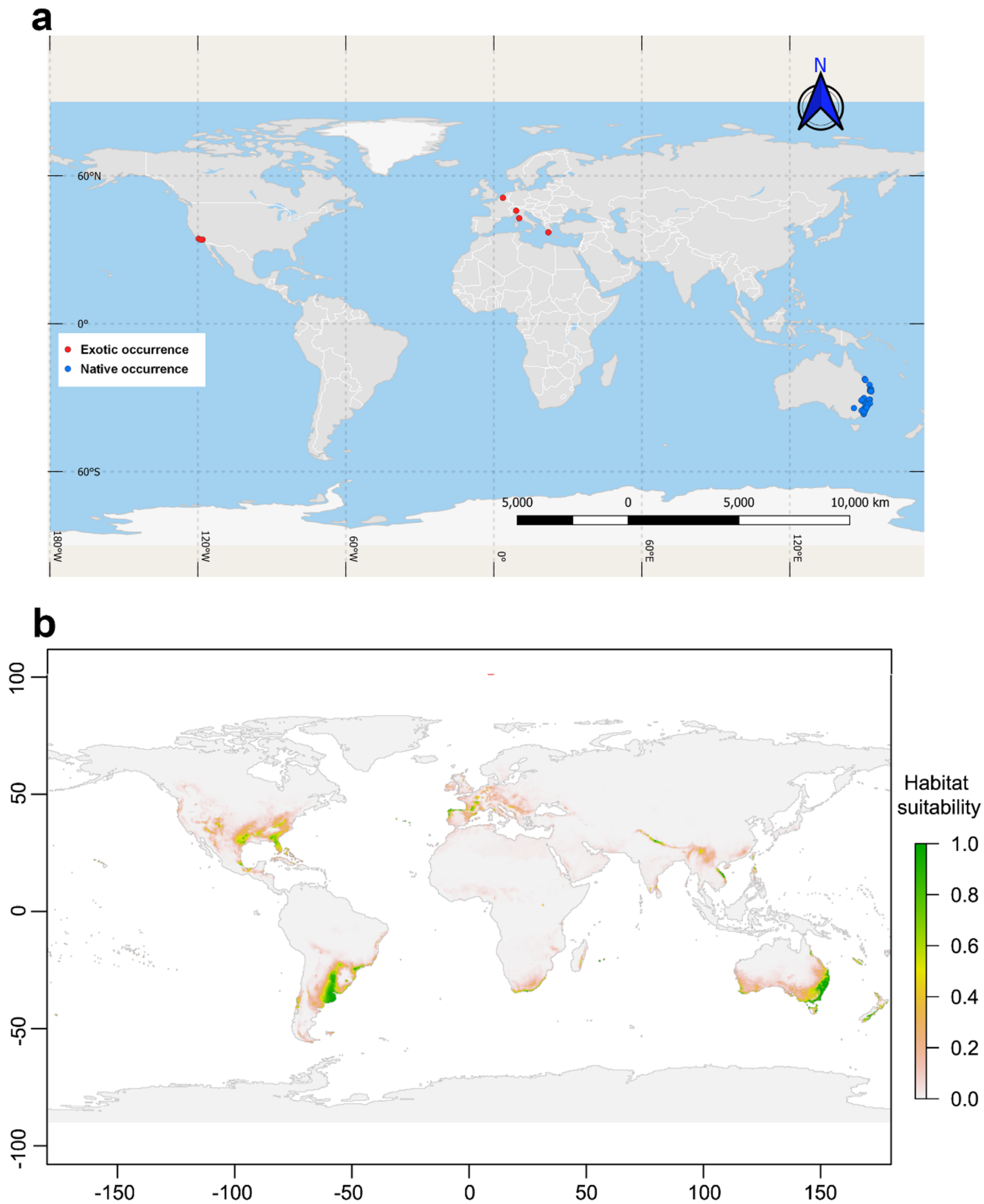

Fig. 2 Map of current occurrence and potential distribution of *Siraton internatus*: **a** global occurrence data of *Siraton internatus*, with exotic records represented by red circles and native occurrences represented by blue circles; **b** potential distribution under current climate. The maps were created using QGIS version 3.22.3 (www.qgis.org) and R version 4.3.2

Table 1 Contribution rates and permutation importance for initial model and final model and VIF values

		Initial model		Final model		First six variables	Final four variables
		Percent contribution	Permutation importance	Percent contribution	Permutation importance	VIF value	VIF value
bio01	Annual mean temperature (°C)	0.5	8.5			1184.622463	
bio02	Mean diurnal range (°C)	1.8	0.1				
bio03	Mean diurnal range (°C)	25.9	0.4	41.1	60.7	7.020420	1.668154
bio04	Mean diurnal range (°C)	18.6	21.5			235.758308	
bio05	Mean diurnal range (°C)	3	6.7			136.115180	
bio06	Min temperature of coldest month (°C)	0.1	1.3				
bio07	Temperature annual range (°C)	0	0				
bio08	Mean temperature of wettest quarter (°C)	2.9	6.9	18.7	22.9	13.207876	1.348044
bio09	Mean temperature of driest quarter (°C)	0.1	0.2				
bio10	Mean temperature of warmest quarter (°C)	0.8	2.6				
bio11	Mean temperature of coldest quarter (°C)	0.8	20.9			1822.377118	
bio12	Annual precipitation (mm)	0.2	1.5				
bio13	Precipitation of wettest month (mm)	0.2	0				
bio14	Precipitation of driest month (mm)	1.7	1.4				
bio15	Precipitation seasonality (mm)	1.5	0				
bio16	Precipitation of wettest quarter (mm)	0.7	0.3				
bio17	Precipitation of driest quarter (mm)	12.2	0.6	38.4	13.5	2.165089	1.927606
bio18	Precipitation of warmest quarter (mm)	0.1	0				
bio19	Precipitation of coldest quarter (mm)	28.8	27.1	1.8	2.9	2.214489	2.163050

10,000 background points, iterating until reaching 500 iterations or a convergence threshold of 0.00001. The default parameter configurations in MaxEnt can result in overly complex or overly simplified models (Warren and Seifert 2011). To identify optimal parameter settings and reduce the risk of overfitting, we employed 'ENMeval' (Kass et al. 2022), which evaluates different combinations of feature classes and regularization multipliers. We used random ten-fold cross-validation to split the datasets into training and test sets, ensuring the model's transferability across different spatial and temporal scenarios. The Akaike Information Criterion with a small sample size correction (AICc) was utilized to select the best model settings. We chose the model parameters that resulted in the lowest delta AICc value, indicating the simplest model with adequate fit (Warren and Seifert 2011). The selected features were linear and quadratic (LQ), with a regularization multiplier set at 0.5, optimizing the balance between model complexity and explanatory power.

Model prediction and map visualization

To address concerns about the impact of study area extent on model performance and predictions, we built upon the model parameters established in the previous section (Low et al. 2021; Amaro et al. 2023). Utilizing known global distribution points with 10-min resolution current climate data, we derived maximum entropy to project global potential distributions at a 10-min resolution. These projections were further refined for specific regions such as Australia and Taiwan at a higher resolution (30-s) and under various future climate scenarios to assess changes over time. Using the logistic output of MaxEnt, we estimated the probability of species presence based on environmental variables (i.e., habitat suitability) for each grid cell. This enabled the generation of potential distribution maps for different time periods and climate scenarios, illustrating the possible impacts on the species' distribution (Figs. 2b, 3, 4, 6; Figs. S5–S28). In addition, we identified potential host plants of *Macrozamia* cycads listed in Table S2, for which occurrence data were retrieved from the Atlas of Living Australia (ALA: http://www.ala.org.au). These data were then overlaid on the maps to visualize their correspondence with the weevil's potential distribution across Australia (Fig. S29). Specifically, for the two reserve areas of Taiwan (CMR and HCR) (Fig. S1), habitat suitability assessments were extracted for different timeframes and scenarios. Scatter plots, created using "ggplot2" (Wickham et al. 2019), helped assess the direct impacts on these

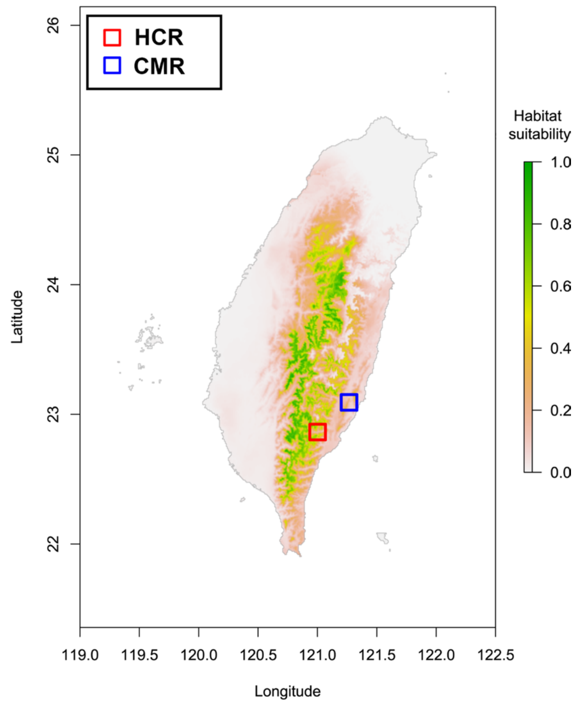

Fig. 4 Potential distribution of *Siraton internatus* in Taiwan. CMR: Coastal Mountain Range; HCR: Taitung Hongye Village Taitung Cycas Nature Reserve. Map were created using R version 4.3.2

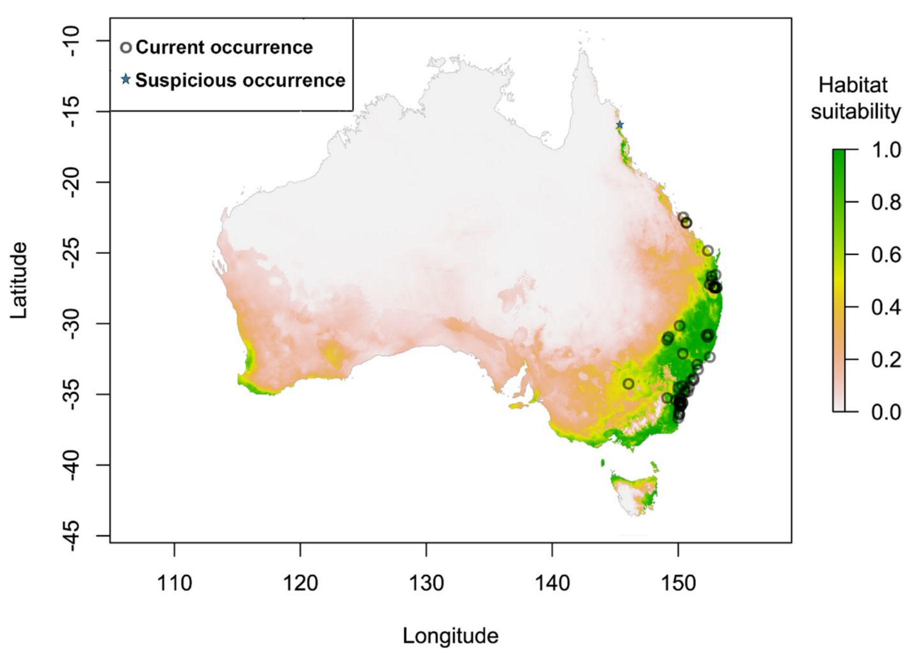

Fig. 3 Potential distribution of *Siraton internatus* in Australia, with current occurrences represented by red cycles and suspicious occurrence represented by blue stars. Map were created using R version 4.3.2

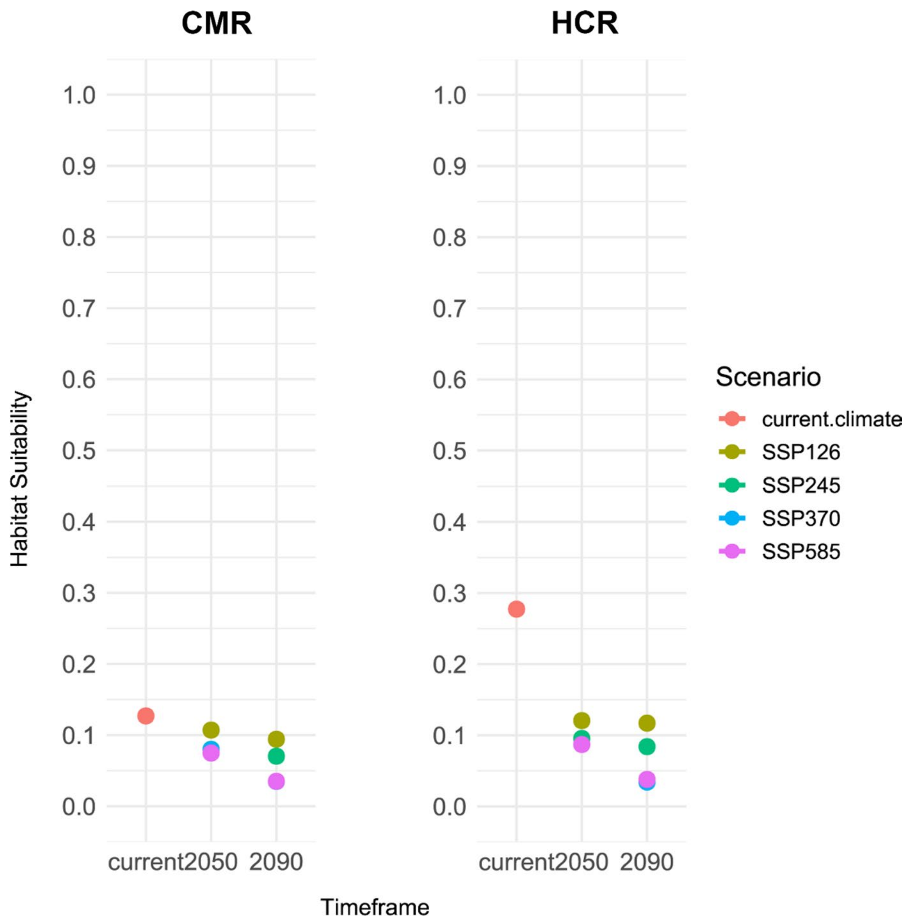

Fig. 5 Habitat suitability of *Siraton internatus* in two Taiwanese cycad reserves under varying climate change scenarios. The graph displays changes in habitat suitability within the Coastal Mountain Range (CMR) and the High Central Range (HCR) across different timeframes (current, 2050, and 2090) and under different Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5). Each point represents the average habitat suitability under a specific climate scenario, illustrating how predicted changes in climate could impact the potential distribution of *Siraton internatus* in these reserves. Figure was created using R version 4.3.2

reserves (Fig. 5). Dominant environmental variables were identified through a jackknifing process (Fig. S3) (Boria et al. 2014), and response curves were generated to examine the effects of individual variables on species presence (Fig. S4). All figures were optimized for clarity using Adobe Photoshop 2021 (Adobe Systems Inc.).

Model validation

To assess the efficacy of our models, we utilized the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Fielding and Bell 1997), which measures the true positive rate against the false positive rate. AUC values span from 0 to 1, where higher values denote better predictive performance of the model (Fig. S2a) (Hernandez et al. 2006; Phillips et al. 2006; Franklin 2010; Peterson et al. 2011; Velasco et al. 2019). Additionally, we calculated the difference between the training and testing AUC values (AUC.diff) to gauge the model's generalizability (Warren and Seifert 2011). A smaller AUC.diff indicates consistent performance across both datasets, suggesting robust generalization capabilities, whereas a larger AUC.diff might indicate potential overfitting to the training data. Furthermore, we applied the continuous Boyce index (CBI) (Boyce et al. 2002; Bellard et al. 2013) to quantify the agreement of the model predictions with the actual presence data. The CBI ranges from -1 to 1, with positive values indicating that the model's predictions align well with observed distributions, and values near zero indicating performance akin to random chance. Omission rates (OR) at 0% and 10% sensitivities were also analyzed to assess the model's precision in predicting known presences of *S. internatus* (Pearson et al. 2006; Peterson et al. 2008; Liu et al. 2013). The model's adequacy is questioned if the default OR exceeds the predicted rate, which could signify an underprediction of known species locations (Peterson et al. 2011). The alignment of the training set OR (depicted by a blue line) with the predicted OR (black line) further served as an accuracy check, with close alignment indicating that the model reliably predicts known occurrences (Fig. S2b) (Radosavljevic and Anderson 2014).

Results

Model performance in predicting *Siraton internatus* potential distribution

Our MaxEnt model underwent rigorous validation, displaying exemplary performance across a range of metrics, confirming its suitability for accurately predicting the potential distribution of S. internatus. Achieving a Delta AICc of 0 and an AICc of 969.9185, the model demonstrated an optimal balance between complexity and fit. This was further evidenced by the incorporation of 10 coefficients, reflecting a sophisticated approach to modeling ecological patterns. The model excelled in validation metrics, evidenced by a high average validation AUC of 0.979265, with an AUC difference of just 0.0120902 between the training and validation sets. This small difference underscores the model's robust generalization capabilities across datasets. Additionally, the 10% training omission rate averaged at 0.145, indicating the model's precision in capturing known species locations within the training data. The continuous Boyce Index values of 0.908 for training and 0.6468 for validation affirm the model's alignment with actual species distributions, suggesting that the predictions are not only accurate but also ecologically meaningful. Visual evaluations (Fig. S2) through omission rate graphs and the ROC curve further affirmed the model's reliability. The omission graph closely matched predicted with observed omissions, highlighting the model's fidelity in representing the species' actual presence across its potential range. Moreover, the ROC curve displayed an impressive training AUC of 0.985, significantly surpassing the threshold for random predictions, which illustrates the model's exceptional predictive power (Franklin 2010; Peterson et al. 2011; Velasco et al. 2019).

Predicting the potential distribution for *Siraton internatus* under the current climate

Our predictions showed that *S. internatus*'s potential global distribution (Fig. 2b) encompasses areas specifically highlighted in Australia (Fig. 3) and Taiwan (Fig. 4). Green zones represented high habitat suitability, red indicated moderate habitat suitability, and white represented low suitability. The weevil's potential global distribution (Fig. 2b) highlights high-risk coastal areas, including regions beyond its native Australian habitat like Argentina, Brazil, Chile, France, Mexico, Nepal, New Caledonia, New Zealand, Philippines, Portugal, South Africa, Spain, Taiwan, the USA, and Vietnam. Figure 3 showed that the highly suitable habitats of *S. internatus* include the coastal regions of northern Queensland to Victoria, southwestern Western Australia and Tasmania. When considering the distribution of potential host plants in the genus *Macrozamia*, overlaid with the weevil's potential distribution, there is a noticeable concentration of suitable habitats along the eastern coast of Australia (Fig. S29). This overlap suggests areas where *Macrozamia* populations could be at risk due to weevil invasion, providing critical information for conservation efforts. Focusing on Taiwan (Fig. 4), our analysis revealed that the high mountain areas exhibit high habitat suitability for *S. internatus*. Contrastingly, the northern and western regions of Taiwan are predominantly characterized by large areas of low suitability, marked as white areas on the map. Notably, when factoring in Taiwanese cycad reserves (Fig. 5), the Coastal Range Taitung Cycas Forest Reserve (CMR) and Taitung Hongye Village Taitung Cycas Nature Reserve (HCR) both show low habitat suitability for *S. internatus* (0.126988 and 0.2773997). The contribution rate of the environmental variables and their permutation importance according to the jackknife test are presented in Table 1 and Fig. S3. Response curves for four selected variables of *S. internatus* are shown in Fig. S4, which all showing unimodal relationships, which indicate the relationship with the habitat suitability and variable values.

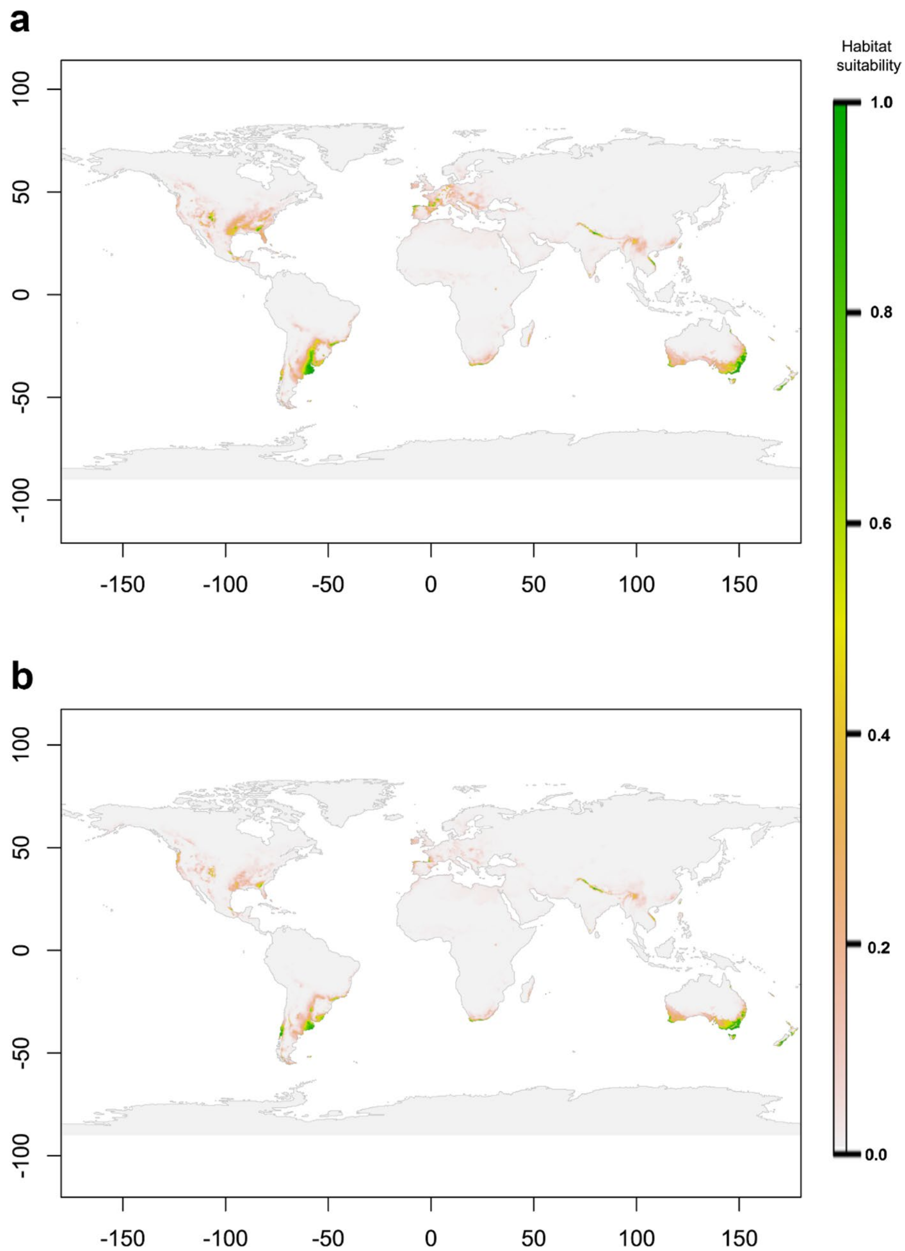

Fig. 6 Potential distribution of *Siraton internatus* under the least and most severe climate change scenarios: **a** SSP1-2.6 in 2090; **b** SSP5-8.5 in 2090. Figure was created using R version 4.3.2

Projection of future potential distribution for weevil under the future climate

Projections of *S. internatus*'s potential distribution under varying SSP climate scenarios are depicted in Fig. 6 and Figs. S5–S28, considering the four climate change scenarios over two-time frames, including the least severe (SSP1-2.6) and most severe (SSP5-8.5) climate change scenarios. Our global analysis revealed that suitable habitats for the species are subject to noticeable variability in response to climate change. Although a general trend of contraction is evident, particularly in regions such as North America and Europe, unique variations are observed in specific locales over the next seven decades. Our projections identify a distinct southward shift in suitable habitats within Australia, reflecting a change from traditional ranges towards new potential habitats further south. Conversely, in Taiwan, particularly within the CMR and HCR regions (Figs. 4, 5), the suitability for *S. internatus* starts from a low baseline and is further exacerbated by climate change, with projections indicating a significant decline to below 0.1 by 2090 under the harsher climate scenarios, signaling a worrying trend towards greater unsuitability. Additionally, distinct expansion of suitable habitats for *S. internatus* was identified along a specific elongated region in the southern Himalayas, notably encompassing areas within Nepal and Bhutan. This linear area of increased habitat suitability stands in stark contrast to the global trend of habitat contraction and indicates potential new refuges for the species in these high-altitude regions despite broader climate-induced pressures.

Discussion

Distribution of *Siraton internatus* in Australia, with discussion on its ecology

Our model predicted the potential distribution of *S. internatus* based on current climatic variables and occurrence data. These predictions align with known occurrence records (Fig. 2 and Table S1), barring Victoria, northern Queensland, Tasmania and southwestern Western Australia. In Victoria, northern Queensland and Tasmania, natural populations of *Macrozamia* are absent. Additionally, southwestern Western Australia is inhabited by another species of *Siraton* (*S. roei* (Boheman,)). A notable report by Hsiao and Oberprieler (2020) reported a suspicious record of *S. internatus* near Cooktown in northern Queensland (Fig. 3), outside its recognized range. Yet, our models do highlight northern Queensland areas like Koombooloomba National Park and Girringun National Park as highly suitable for this weevil. The presence of several botanical gardens in northern Queensland raises the possibility of accidental introductions via cycad bonsais. As Hsiao and Oberprieler (2020) pointed out, certain specimens from the Australian National Botanical Garden in Canberra, where native cycads are absent, suggest inadvertent introductions. The same could apply to northern Queensland, although no subsequent specimens have been discovered. Hsiao and Oberprieler (2020) mapped seven potential *Macrozamia* cycad hosts (Table S2) for *S. internatus*, with *M. polymorpha* subsequently confirmed as a host in Hsiao and Oberprieler (2021). Our predictions showed a considerable overlap between these cycads and *S. internatus*'s potential distribution, supporting earlier findings. Furthermore, we identified 19 new potential *Macrozamia* hosts from eastern Australia for *S. internatus* (Table S2) based on its potential distribution. This indicates that *S. internatus* can potentially infest most *Macrozamia* species in their natural habitats.

Australia's domestic botanical or home gardens are notably susceptible to cycad-attacking weevils. The threat is magnified in gardens within the native cycad and weevil range, such as the Cairns Botanic Gardens, Brisbane Botanic Gardens, City Botanic Gardens in Queensland, the North Coast Regional Botanic Garden, Orange Botanic Gardens, and Royal Botanic Garden Sydney in New South Wales, and the Australian National Botanic Gardens in the Australian Capital Territory. These botanical gardens, due to their diverse cycad collections, can be prime weevil habitats. For example, Kennedy (1992) reported the loss of several *Encephalartos* plants and a mature *Zamia furfuracea* due to a large infestation of *S. internatus*. Small-scale occurrence of *S. internatus* have also been reported at the Australian National Botanical Garden in the Australian Capital Territory (Hsiao and Oberprieler 2020). Additionally, Maria Walford-Huggins, who established an impressive collection of endemic and exotic cycads in Julatten, northern Queensland in the 1980s (Birkbeck and Birkbeck 2014), recorded an infestation of *Demyrsus digmon* Hsiao and Oberprieler 2020 on *Encephalartos* cycads (Hsiao and Oberprieler 2020). Our results indicated that both infestation events by *S. internatus* occurred within the potential distribution range of the weevil. Furthermore, our future projection covered four different climatic scenarios over two future time frames, highlights the ongoing vulnerability of artificial facilities in eastern Australia to *S. internatus* (Figs. 6, S5–S28). However, we previously considered that the response curves of the model (Table 1 and Fig. S5) can provide insufficient biological data of the weevil, but Smith and Sonto (2020) caution against over-interpreting the importance of specific climatic variables based solely on model accuracy. Overall, our findings offer crucial insights for cycad conservation and managing *S. internatus* infestations, beneficial for botanical gardens, the horticultural industry, and cycad enthusiasts.

Global invasion of *Siraton internatus* and its potential impacts to cultivated and wild cycads

While *S. internatus* originates from Australia, the weevil's suitable habitats under the current climatic conditions stretch beyond its native confines. Areas of pronounced risk include locales spanning Argentina, Brazil, Chile, France, Mexico, Nepal, New Caledonia, New Zealand, Philippines, Portugal, South Africa, Spain, Taiwan, USA, and Vietnam (Fig. 2). Notably, many of these regions harbor native cycad species: Mexico boasts 26 species, New Caledonia one, Philippines two, South Africa 24, the USA three, Taiwan one, and Vietnam seven (detailed in Table S3). This overlap underscores the invasive threat *S. internatus* poses to cycad conservation. This threat isn't limited to wild cycads. Cultivated cycad plants, vital for ex-situ conservation of endangered cycad species, are equally vulnerable, especially when situated in or near these high-risk zone (Westwood 1886; Glass 1980; Kennedy 1992, 2011; Oberprieler and Caldara 2012). Historical data evidences the weevil's capacity to inflict significant damage in botanical or domestic gardens and nurseries. A multitude of these risk areas are proximate to botanical gardens, intensifying concerns about accidental biological invasions. Examples include the La Plata Botanical Garden and E.N.Orfila Botanical Garden in Argentina, the Botanical Gardens of Porto Alegre and Jardim Botânico De Caxias Do Sul in Brazil, the Nacional de Viña del Mar Botanical Garden and Parque Paraiso Escalante in Chile, the Arquebuse Botanical Garden and Botanical Garden of Lyon in France, the Rock Garden of Liwang and Banke Botanical Garden in Nepal, the Parc Zoologique et Forestier Michel Corbasson and de Félix et Janine BOLE Botanical Garden in New Caledonia, the Timaru Botanic Gardens and Christchurch Botanic Gardens in New Zealand, the Baguio Botanical Garden in Philippines, the Tropical Botanical Garden of Lisboa and Jardim Botânico do Porto in Portugal, the Makana Botanical Gardens and Durban Botanic Gardens in South Africa, the Jardín Botánico Atlántico de Gijón and Barakaldo Botanical Garden in Spain, the Botanical Garden of National Museum of Natural Science in Taiwan, the San Diego Botanic Garden and South Coast Botanic Garden in California and McKee Botanical Gardens in Florida in USA, and the Phong Nha Botanic Garden in Vietnam. Furthermore, botanical gardens, pivotal for biosecurity, can inadvertently act as gateways for pest and pathogen invasions (Wondafrash et al. 2021). Thus, they might inadvertently catalyze the establishment of weevil populations in surrounding environments.

However, it's noteworthy that only a few isolated areas are marked as high risk. This suggests a low likelihood of *S. internatus* evolving into a dominant global cycad pest akin to the cycad blue butterfly or cycad scale insect. Interestingly, despite multiple invasions spanning over a century, *S. internatus* hasn't entrenched itself in foreign territories, causing localized damages rather than widespread establishment (Westwood 1886; Glass 1980; Kennedy 1992, 2011; Oberprieler and Caldara 2012). This observation casts doubt on the accuracy of the pest threat ranking system proposed by Tang and Oberprieler (2006), which might have overestimated the threat posed by Australian cycad-boring weevils.

The evaluation of invasive threat of *Siraton internatus* to Taiwan's endemic cycads

Taiwan, an East Asia island celebrated for its rich biodiversity despite its modest size, is home to the singular endemic cycad species, *Cycas taitungensis* (Shao and Chung 2022). Restricted to two petite populations, this species is safeguarded within two nature reserves: Coastal Range Taitung Cycas Forest Reserve (CMR) and the Taitung Hongye Village Taitung Cycas Nature Reserve (HCR) (Fig. S1). Beyond the challenges of habitat destruction, illegal harvesting, and horticultural trade, *Cy. taitungensis* grapples with invasive threats like the cycad blue butterfly and the cycad aulacaspis scale insect (Chang 1989; Chao and Lai 2005). These challenges have led to its classification as endangered (EN) on the latest IUCN Red List (Bösenberg 2022). To gauge the potential fallout of the Australian cycad-attacking weevils on this indigenous species, we embarked on a focused assessment of the weevil's habitat compatibility within these Taiwanese nature reserves. Overlaying the confines of these reserves onto a map delineating the weevil's suitable habitats in Taiwan (as seen in Fig. 5), it's evident that both CMR and HCR have low habitat suitability for *S. internatus* establishment, which is beneficial for the survival of *Cy. taitungensis*. However, occasional infestation events of *S. internatus* may still occur in some local botanic gardens, as observed previously (Westwood 1886; Glass 1980; Kennedy 1992, 2011; Oberprieler and Caldara 2012). Furthermore, the growing trend of cultivating cycad bonsai for decorative purposes in Taiwan heightens the risk of unintentionally ushering in the Australian cycad weevil. Although there's no documented instance of *Cy. taitungensis* serving as a host for *S. internatus*, recent studies spotlighting species delimitation draw parallels between *Cy. taitungensis* and *Cy. revoluta* (Chang et al. 2022). Given that the latter has been a known host for *S. internatus*, the potential vulnerability of *Cy. taitungensis* becomes palpable. This research unveils a fresh, looming menace to the conservation endeavors for *Cy. taitungensis*. Coupled with the onslaught from existing invasive pests, its limited population, isolated habitats, and unlawful trade, the prospect of *Cy. taitungensis*'s survival dims considerably should *S. internatus* gain a foothold.

Impact of climate change on the distribution of *Siraton internatus*, with suggestions to future cycad conservation and pest management

Climate change is reshaping global ecosystems, leading to significant alterations in species distribution patterns (Nogué et al. 2009; Naimi et al. 2022), which in turn challenges *S. internatus* habitats worldwide. Our ecological niche modeling indicates a global trend of habitat contraction for *S. internatus*, with notable exceptions highlighting the complex nature of these shifts. Specifically, we observe expansion of suitable habitats in regions such as southern Chile and the southern Himalayas, including Nepal and Bhutan (Fig. 6, Figs. S5–S12). These areas represent unexpected refuges where *S. internatus* could potentially thrive amidst global contractions. Conversely, in Australia (Figs. S13–20), the weevil's native habitats, there's a discernible southward shift in suitable habitats, reflecting climate-driven migration within its endemic range. This adaptation suggests that while traditional habitats may become less viable, new areas could emerge as suitable, necessitating updates to current management and conservation strategies to account for these shifts. Moreover, while our modeling efforts provide a critical foundation for understanding these distributional changes, following insights from Smith and Santos (2020), we acknowledge the importance of increasing sample size in future modeling efforts. Enhanced sample sizes are crucial for a more reliable inference of variable importance and ensuring more accurate and robust predictions of habitat suitability and invasion risks. This becomes especially significant as we continue to adapt our conservation strategies in response to shifting ecological niches and emerging threats.

The contrasting patterns of habitat contraction globally, with expansions in specific locales such as Chile and the southern Himalayas, and shifts within Australia, underline the need for nuanced conservation approaches. These should be tailored to local conditions and include both preventive measures in newly suitable areas and adaptive strategies in regions experiencing habitat shifts. Enhanced monitoring and biosecurity are crucial, particularly in regions facing new risks from *S. internatus* expansion, to prevent its spread to ecosystems previously unaffected by this pest. Therefore, our findings underscore the imperative for a multifaceted approach to conservation in the face of climate change, balancing the need to address habitat contractions globally with the necessity to manage emerging threats and opportunities in specific regions.

Conclusion and future works

This study has investigated the distribution and potential invasion risks of the trunk-boring cycad weevils, *S. internatus*, with a focus on both its native territory in Australia and its potential impacts globally, particularly in Taiwan. Modeling habitat suitability under current and future climate scenarios revealed a nuanced response to climate change, with global habitat contractions anticipated, alongside localized expansions and shifts, such as in southern Chile and the southern Himalayas. Given these insights, we continue to recommend stringent quarantine measures on cycad imports and advocate for the regulation of cycad caudex exports from Australia to prevent further spread of *S. internatus*. To refine future predictions, extensive faunistic surveys of *S. internatus* should be prioritized. Furthermore, attention should be given to the other three known Australian cycad-attacking weevils: *S. roei*, *Demyrsus meleoides* Pascoe, and *D. digmon*. The invasion of *D. meleoides* into regions like Italy, South Africa, and the UK, coupled with its affinity for African *Encephalartos* cycads, underscores its economic significance (Covassi 1974; Oberprieler 1995; INVASIVE.ORG 2023). Employing alternative models (e.g., physiologically based demographic models, (Ponti et al. 2021)), can enhance our understanding of the potential invasion when more data become available. Future research should explore the potential spatial overlap and interaction between *S. internatus* and various cycad species. This includes a detailed investigation into the weevil's impact on both known and potential cycad hosts, enhancing our understanding of its ecological dynamics and informing targeted conservation efforts. As a pioneering effort in this niche field, we aim to lay the groundwork for advanced cycad conservation strategies and the management of invasive pests like *S. internatus*. This study underscores the necessity for a multifaceted approach in studying and mitigating the impacts of invasive species on global cycad populations. Highlighting the importance of continued research, monitoring, and fostering international collaboration, particularly in areas such as biosecurity measures and conservation strategies, is essential.

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Author contributions YH designed the study and drafted the manuscript; JRL analyzed the data and review the manuscript. All authors contributed to the study conception, design, and approved the final version of manuscript.

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Declarations

Conflict of interest The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability All data generated and analyzed during this study are included in this published article and its supplementary information files.

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