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Research

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Modeling the Distribution of the Invasive Alien Cycad Aulacaspis Scale in Africa Under Current and Future Climate Scenarios

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Abstract

The cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi (Hemiptera: Coccoidea: Diaspididae), is native to Southeast Asia but an invasive pest of the gymnosperm order Cycadales in many parts of the world. *Aulacaspis yasumatsui* was recently reported on the cycad genus *Encephalartos* in South Africa and is currently categorized as a 'prohibited terrestrial invertebrate' in the invasive species legislation, National Environmental Management: Biodiversity Act, 2004 (NEM:BA). *Encephalartos* is endemic to Africa, and 11 species are listed as critically endangered and four species as endangered. Seeing the limited distribution of *A. yasumatsui* in South Africa and only one unconfirmed record from the Ivory Coast, understanding the potential distribution range is essential for control and management. Here we model the potential distribution of *A. yasumatsui* under current and future climate scenarios in Africa, with a focus on South Africa. Future climatic scenarios were simulated using a bioclimatic software, CLIMEX. The model indicates that, under the current climatic scenario, all 17 African countries possessing *Encephalartos* are susceptible to *A. yasumatsui* establishment. However, under climatic change, the suitability decreases for large parts of Africa. In South Africa, 93% of the winter rainfall areas, and 90% of the temperate, summer rainfall areas are suitable for *A. yasumatsui* establishment. In this study, we highlight the urgent need for regulation, management, and research on *A. yasumatsui* in African countries with native cycads.

Key words: climate change, CLIMEX, *Encephalartos*, *Aulacaspis yasumatsui*, risk analysis

Cycads (Cycadales), commonly known as 'sago palms', are characterized as 'living fossils' due to their long evolutionary history (Brenner et al. 2003, Marler and Moore 2010, Salas-Leiva et al. 2013). Cycads are found across much of the subtropical and tropical parts of the world and are successfully growing in a variety of environmental conditions, from deserts to rain forests (Bermingham et al. 2005). Cycads are among the most imperiled plant groups and the majority of the 356 species (10 genera) are listed as threatened (Calonje et al. 2019, IUCN 2019). South Africa, with 38 species, is considered one of the global hotspots for cycad diversity (Bamigboye 2018). Of these, 37 species are from the genus *Encephalartos* and 76% of these are endemic to South Africa (Golding 2002, Government gazette 2017). Twelve out of the 37, i.e., nearly 32% of the *Encephalartos* species that occur in South Africa, are categorized as 'Critically Endangered', with three considered as 'Extinct in the Wild' (Raimondo et al. 2009).

An invasive alien scale insect, *Aulacaspis yasumatsui* Takagi (Hemiptera: Coccoidea: Diaspididae), commonly known as the cycad aulacaspis scale, can have devasting impacts on cycads, and the first report from the Ivory Coast (Germain and Hodges 2007) and later from South Africa (Nesamari et al. 2015) are of concern. *Aulacaspis yasumatsui* is native to South East Asia and was first described in 1972 in Thailand (Takagi 1977). The first report of *A. yasumatsui* outside of its native range was from Florida (United States) in 1996 (Howard et al. 1999). Subsequently, it has spread to other states and neighboring Mexico (Haynes 2005, González-Gómez et al. 2016, Normark et al. 2017). Currently, *A. yasumatsui* is listed as invasive in Puerto Rico (CABI, EPPO 2000, Invasive Species Specialist Group (ISSG) 2011), California, Florida, Hawaii, Guam, Northern Mariana Islands, Palau (Invasive Species Specialist Group 2011), and South Africa (Nesamari et al. 2015). *Aulacaspis yasumatsui* is most likely to move into new regions via the horticultural trade (Global Invasive Species Database 2020). Once introduced, it has the ability to spread rapidly, and control is difficult (Haynes and Marler 2005). Controlling an alien invasive species at the early stages of invasion is most cost-effective and has

the potential to limit impacts (Geerts et al. 2016, Geerts et al. 2017). Consequently, if *A. yasumatsui* is not managed in a timely manner, it is likely to devastate entire populations, since it can destroy mature cycads in a few months (Howard et al. 1999).

Climate change influences the naturalization and spread of invasive alien species in their novel habitats (Ekesi et al. 2016, Paini et al. 2016, Walsh et al. 2016). In particular, for insects, since they are poikilothermic and temperature plays a crucial role in their survival and dispersal. Increasing temperatures can alter physiological characteristics and population dynamics such as natality, mortality, development rate, as well as geographical distribution (Bellard et al. 2013, Duan et al. 2014, Yousuf et al. 2014). Wei et al. determined the most favorable environmental conditions for *A. yasumatsui* and found that areas with a mean temperature between 15 and 20°C in the driest quarter and a mean temperature of 25 to 28°C in the wettest quarter are most favorable for establishment (Wei et al. 2018). Here we build on this and refine the predictions for Africa and South Africa specifically. At present, *A. yasumatsui* has a localized distribution in three South African provinces: Gauteng, KwaZulu-Natal, and Limpopo (Nesamari et al. 2015). Despite this, in previous models, Gauteng is a part of South Africa predicted to be climatically unsuitable (Wei et al. 2018). Other than these records, there are no reports of further spread in South Africa or other African countries. Therefore, understanding the potential distribution of *A. yasumatsui* in South Africa and other African countries and how this is influenced by changing climate is important for monitoring, management, and prevention of further spread of this species. Furthermore, these predictions will aid in guiding where preventive and control measures should be implemented.

In this study, we used a bio-climatic software, CLIMEX to identify climatically favorable regions for *A. yasumatsui* and determine the potential distribution and population dynamics of *A. yasumatsui* under current and future climate scenarios.

Materials and Methods

Aulacaspis yasumatsui Distribution Modeling

Aulacaspis yasumatsui occurrence data were obtained from the Centre for Agriculture and Bioscience International (CABI, www.cabi.org) datasets, the published literature as well as through personal communication with experts. We used CLIMEX, a bio-climatic software program (version 4.0.2) (https://www.hearne.software/Software/CLIMEX-DYMEX/) that incorporates pest life history parameters (see CLIMEX parameter fitting section) for building a model to predict the climate suitability of Africa for *A. yasumatsui* establishment. In contrast, Wei et al. (2018) used 'MaxEnt' for modeling cycad aulacaspis scale distribution, for which they used a number of environmental factors with presence-only data to yield the potential distribution. MaxEnt is used to find the probability distribution of maximum entropy, subject to limitations imposed by the environmental conditions and the observed spatial distribution of a species. Thus, the output satisfies these constraints by means of the maximum entropy distribution (Jaynes 1957, Phillips et al. 2006). In contrast, CLIMEX uses the eco-climatic index (EI), which quantifies habitat suitability for a target species in a specific location, based on the climate. In doing so, CLIMEX incorporates species growth thresholds to generate distribution models. We incorporated the Growth Index (GI), which is an indicator of population growth rate and is based on a number of parameters, namely, temperature, substrate, soil moisture, light exposure, radiation, and diapause ability (Hill et al. 2014, Kriticos et al. 2015, Byeon et al. 2017).

Potentially favorable regions for the establishment of *A. yasumatsui* were modeled using the 'Compare Locations (1-species, extended)' function of CLIMEX. The 'wet tropical' template was used as baseline and values were iterated to match the current known distribution. CLIMEX utilizes two factors, i.e., growth (temperature and soil moisture) and stress (cold, heat, wet, and dry) to determine potentially favorable regions for establishment. It combines these two values to provide an EI value, which indicates the extent of suitability for the establishment within a range of 0–100. Higher EI values indicate higher climatic suitability for *A. yasumatsui* growth and survival. Based on the EI values, the areas were categorized as marginal (<25), suitable (25–50), highly suitable (50–75), and optimal (>75) for survival. The generated EI values are independent of the host availability in any given region.

Meteorological data for the running of the CLIMEX model was obtained from CliMond (10' gridded dataset, https://www.climond.org/Core/Authenticated/Climex.aspx). Potentially favorable regions for *A. yasumatsui* establishment under the current climatic scenario were modeled using baseline climatic data (30-yr averages of monthly values for daily minimum and maximum temperature (°C), relative humidity (%) at 0900 and 1500 hours (local time), and monthly precipitation (mm), centered on the year 1975). For future climatic scenarios (2030, 2050, 2070, 2080, 2090, and 2100), CLIMEX was run with the 'A1B group' of the climate dataset, following the IPCC-SRES (Solomon et al. 2007).

CLIMEX Parameter Fitting

The values for the parameters governing the *A. yasumatsui* distribution in a given area were obtained from published literature and some values were iterated (Table 1). Soil moisture has an indirect effect in governing the survival of herbivorous insects. If the soil suffers from water scarcity, it has a direct impact on plants, which, in turn, affects the plant-dependent insects (Pons and Tatchell 1995,

Table 1. CLIMEX parameter values for *Aulacaspis yasumatsui* modeling

Parameters	Mnemonic	Values
Limiting low temperature	DV0	8
Lower optimal temperature	DV1	25
Upper optimal temperature	DV2	28
Limiting high temperature	DV3	35
Limiting low soil moisture	SM0	0.5
Lower optimal moisture	SM1	1
Upper optimal moisture	SM2	1.5
Limiting high moisture	SM3	2
Cold stress temperature threshold	TTCS	8
Cold stress temperature rate	THCS	0
Cold stress degree-day threshold	DTCS	2.5
Cold stress degree-day rate	DHCS	−0.002
Cold stress temperature threshold average	TTCSA	0
Cold stress temperature rate average	THCSA	0
Heat stress temperature threshold	TTHS	36
Heat stress temperature rate	THHS	0.5
Heat stress degree-day threshold	DTHS	0
Heat stress degree-day rate	DHHS	0
Dry stress threshold	SMDS	0.1
Dry stress rate	HDS	−0.005
Wet stress threshold	SMWS	2.5
Wet stress rate	HWS	0.002
Model time set	MTS	7
Cold stress degree-day threshold temperature	DVCS	8
Heat stress degree-day threshold temperature	DVHS	35
Degree days per generation	PDD	538

Hale et al. 2003, Foote et al. 2017). Thus, the soil moisture threshold (SM0), optimum lower (SM1), optimal higher soil moisture (SM2), and upper soil moisture (SM3) values were set at 0.5, 1.0, 1.5, and 2.0, respectively. SM3 was set at 2.0 as *A. yasumatsui* prefers monsoon fed areas in South East Asia (CABI 2019). High soil moisture also hinders the growth of cycads—a primary host—which, in turn, affects the growth of *A. yasumatsui* (William 1995).

Temperature Index

Temperature plays a vital role in governing insect growth and development (Bale et al. 2002, Menéndez 2007, Tomasz and Jacek 2013). The lower threshold temperature for the development of *A. yasumatsui* was set at 8°C (Cave et al. 2009). Based on Ravuiwasa et al. (2012), the lower and upper optimal temperatures (DV1 and DV2) were set at 25 and 28°C, respectively. The upper limiting temperature was set at 35°C to match the current known distribution of the *A. yasumatsui*.

Stress Parameters

Based on the current global distribution, the cold stress temperature threshold (TTCS) was set at 8°C. Cold stress degree-day threshold (DTCS) was set to 2.5°C and cold stress degree day rate (DHCS) was set to –0.002 to include the incidence in the colder regions of Europe. Aulacaspis yasumatsui occurs in the humid tropics; thus, the heat stress temperature threshold (TTHS) was set to 36°C and heat stress temperature rate (THHS) to 0.5°C. These higher temperatures act as a limiting factor for the growth of A. yasumatsui. The dry stress threshold (SMDS) was set at 0.1, since when weekly soil moisture level falls below this range, host plants will wilt and A. yasumatsui will experience drought stress. The dry stress rate (HDS) was set at –0.005. At this rate, A. yasumatsui will experience stress when the soil moisture falls below the SMDS limit. The wet stress threshold (SMWS) was set at 2.5, and the wet stress rate (HWS) was set at 0.002. Aulacaspis yasumatsui will experience stress if the soil moisture exceeds the SMWS limit at the rate of HWS. These parameters influence *A. yasumatsui* establishment in high rainfall areas.

Growth Index

As *A. yasumatsui* is already present in South Africa, it is vital to understand the factors governing growth and development. We utilized the CLIMEX model to generate the GI for a number of locations in South Africa. This index is helpful in understanding the various parameters influencing the population dynamics of *A. yasumatsui* in a given area and allows for the identification of the season with the highest mortality rates, which, in turn, can inform management strategies.

The outcome of the model was validated with already published reports on *A. yasumatsui* occurrence in both the native and invaded regions by visual comparison with the CABI distribution map (Watt et al. 2009, CABI 2019). The CLIMEX input parameters were finalized when the generated output map encompassed all the known global localities of *A. yasumatsui*. The GI was generated using CLIMEX for some of the already established regions, namely, Indonesia, Taiwan, and Florida, as well as for the newly invaded areas in South Africa. Our model accurately covered all the regions where *A. yasumatsui* exists, thus validating it for future scenarios.

Results

Potential Distribution of *A. yasumatsui* Under Current Climate Scenarios

Our model revealed that out of the 54 African countries, 51 countries are at least partially suitable for *A. yasumatsui* establishment. Under the current climatic scenario, all 17 African countries with indigenous *Encephalartos* species are suitable for *A. yasumatsui* establishment (48% are marginally suitable, 36% are suitable, 15% are highly suitable, and 1% is optimal). The highest EI (85) was found for the Democratic Republic of Congo, followed by the other central African countries with humid tropical climates. Similarly, the eastern parts of Madagascar and the east coast of South Africa are optimal for *A. yasumatsui* (Fig. 1). In South Africa, 93% of the winter rainfall areas and 90% of the temperate summer rainfall areas are potentially suitable for *A. yasumatsui* establishment. The highest EI (55) was observed in KwaZulu-Natal and Eastern Cape, with Mpumalanga, Western Cape and Limpopo also possessing high climate suitability and the Northern Cape, North West, and Free state provinces being unsuitable (Fig. 2).

Future Invasion Risk of *A. yasumatsui* Under Climate Change

With the change in climate, the majority of the central African nations—which are highly favorable for establishment in the current climatic scenario—will become gradually less favorable, but *A. yasumatsui* will still be able to establish (Fig. 3). For example, under climatic change, the predicted EI value for the Democratic Republic of the Congo drops from 82 in 2030 to 21 in 2100. In Madagascar, some of the western parts become unsuitable while the 'optimal' eastern areas drop to 'suitable' (Fig. 3). Climatic conditions of six countries, namely, Mali, Burkina Faso, Gambia, Chad, Namibia, and Botswana becomes completely unfavorable (EI 0) for establishment in 2100 and for another six countries (Senegal, Guinea Bissau, Togo, Benin, Sudan, and Somalia), only a small region is potentially suitable for *A. yasumatsui* establishment by 2100.

In South Africa, with a change in climate, the favorableness for establishment is reduced in the Western Cape, Eastern parts of Limpopo, Mpumalanga, KwaZulu-Natal, and in the Eastern Cape (Fig. 4). The Gauteng, North West, and the major part of the Free State province—possessing favorable climatic conditions under the current climatic scenarios—will become completely unfavorable (EI

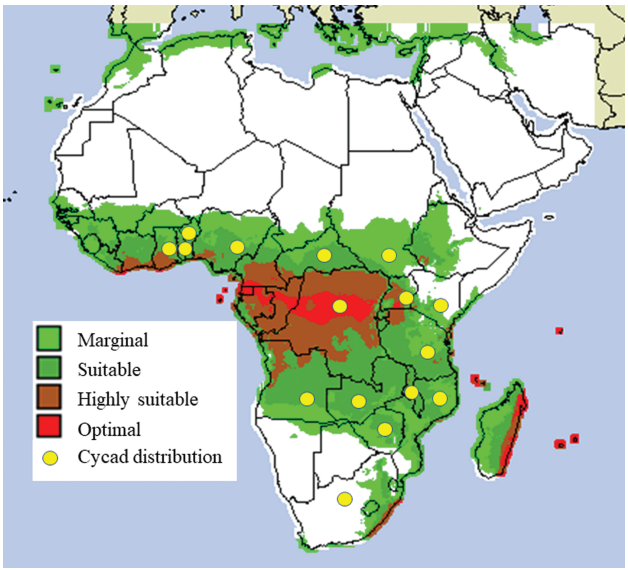

Fig. 1. Potential favorable regions for the establishment of *Aulacaspis yasumatsui* under current climatic scenarios. ● indicates countries with the cycad *Encephalartos* genus.

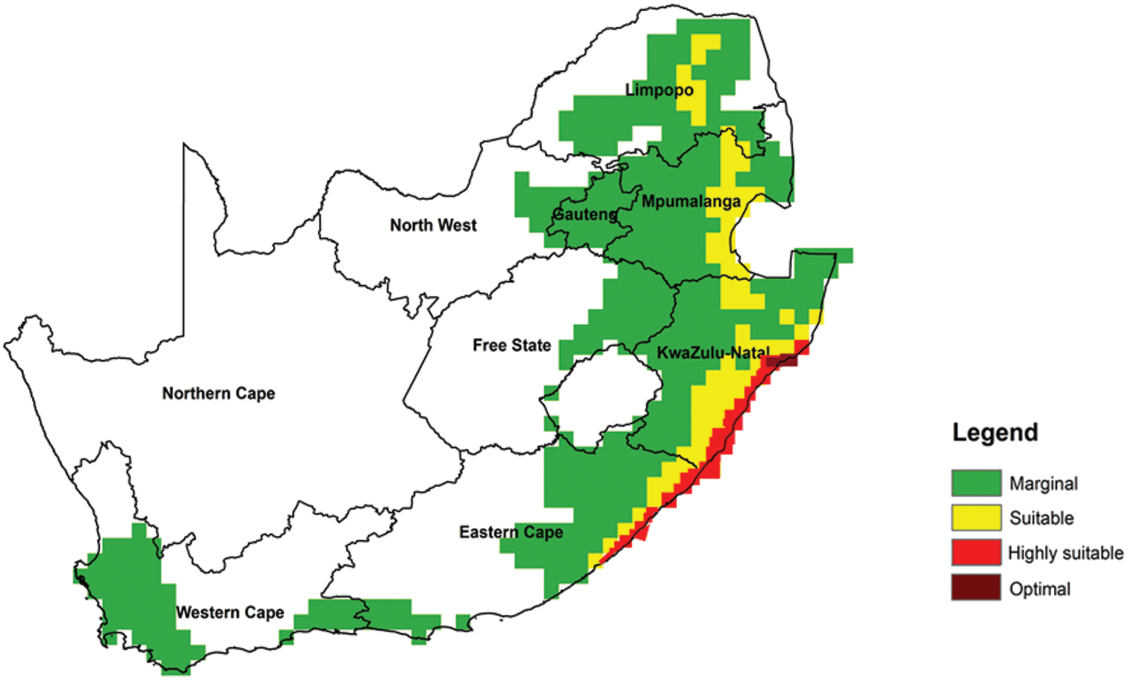

Fig. 2. Potential favorable regions for the establishment of *Aulacaspis yasumatsui* in South Africa under the current climate.

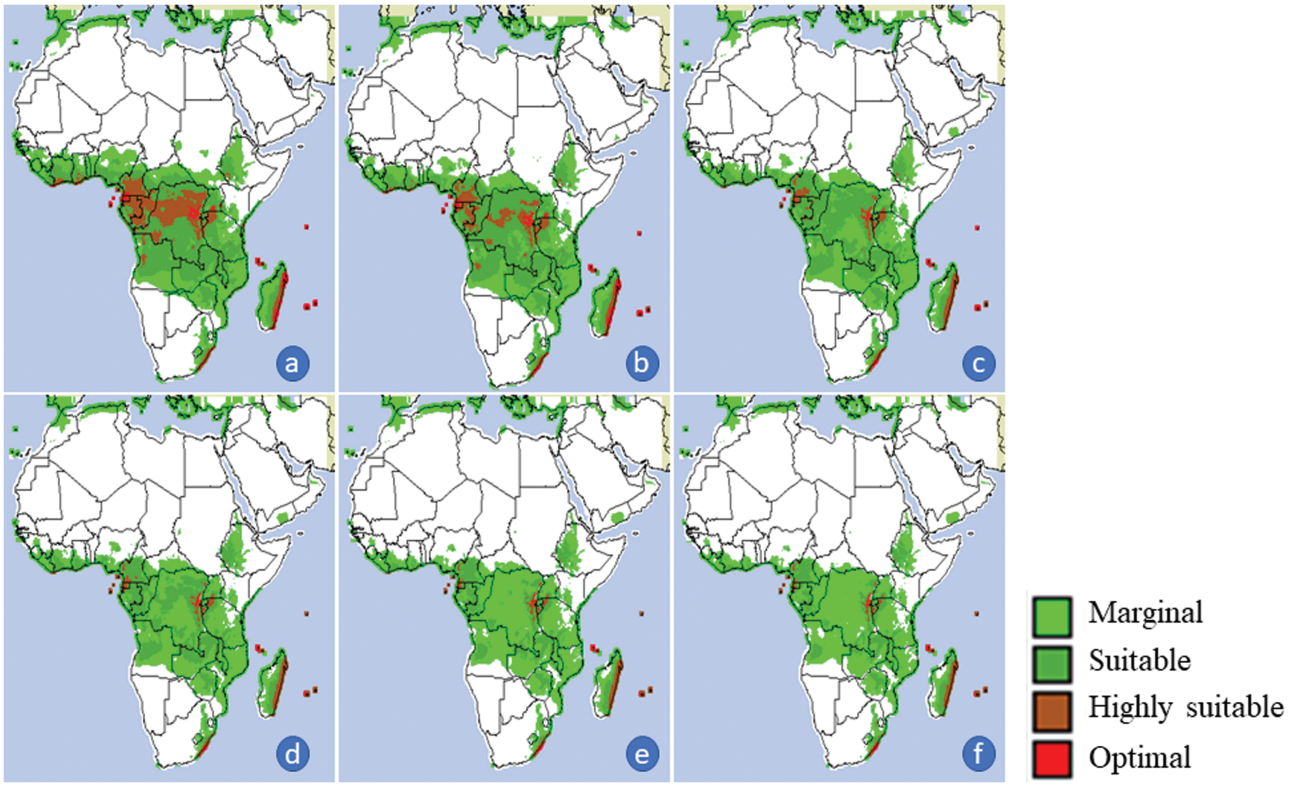

Fig. 3. Potential favorable regions for the establishment of *Aulacaspis yasumatsui* under future climatic conditions (a) 2030, (b) 2050, (c) 2070, (d) 2080, (e) 2090, and (f) 2100.

0) by 2100. On the contrary, western parts of Kwazulu-Natal remain favorable (Fig. 4).

Whilst five African countries become completely unfavorable under future climate change predictions, we predict that *A. yasumatsui* will complete more generations per year in areas that will become less suitable or even marginally suitable. In South Africa, *A. yasumatsui* is predicted to complete approximately 11 generations per year by 2100 compared to nine generations per year

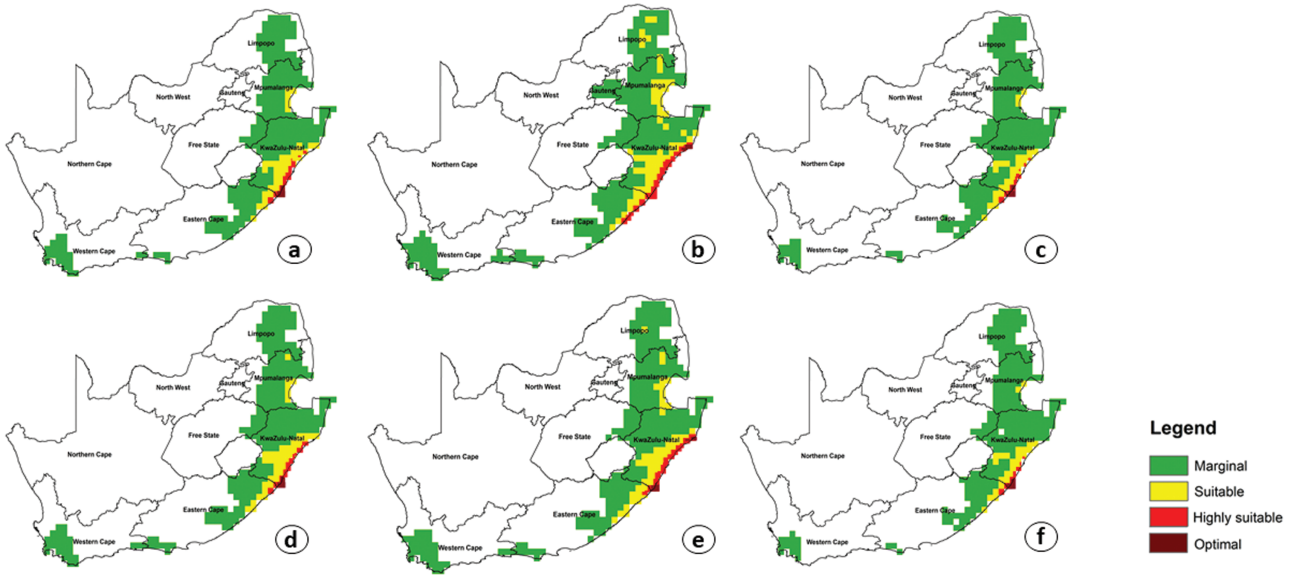

Fig. 4. Potential favorable regions for the establishment of *Aulacaspis yasumatsui* in South Africa under future climatic conditions (a) 2030, (b) 2050, (c) 2070, (d) 2080, (e) 2090, and (f) 2100.

Table 2. EI and number of generations (Gen) predicted for *Aulacaspis yasumatsui* establishment under changing climatic conditions

Province	Location	Present		2030		2050		2070		2080		2090		2100	
	Lat/Long	EI	Gen	EI	Gen	EI	Gen	EI	Gen	EI	Gen	EI	Gen	EI	Gen
KwaZulu-Natal	−28.42; 32.42	71	9.2	66	10.0	62	10.5	56	10.9	53	11.1	48	11.4	45	11.6
Limpopo	−23.92; 29.75	25	5.6	25	6.6	25	7.2	24	7.8	22	8.1	19	8.6	18	8.9
Western Cape	−33.92; 19.08	13	4.0	13	5.3	13	5.6	13	5.9	13	6.1	13	6.3	11	6.5

under current climatic conditions (Table 2). Similarly, an increase in the number of generations for *A. yasumatsui* is predicted for other parts of the African continent (Fig. 5).

Annual GI of *A. yasumatsui*

The weekly GI varies across South Africa. In KwaZulu-Natal, the highest weekly growth is predicted during spring and summer (November to March) with a decrease towards autumn. During these months, lower temperature and atmospheric moisture are predicted to act as a limiting factor for growth and development (Fig. 6), similar to other invaded regions (Fig. 7). This pattern holds for the less suitable summer rainfall areas of the country. On the contrary, in the Western Cape, the highest weekly growth is predicted to be in winter. During winter, the increase in atmospheric moisture, due to high rainfall, favors the growth of *A. yasumatsui* (Fig. 6).

To affirm the accuracy of our generated model, the annual GI was generated for South East Asia and Florida, as *A. yasumatsui* is already well established here, and population dynamics have been studied in these areas. In Indonesia, year-round climatic conditions favor the establishment of *A. yasumatsui*, whereas in Taiwan, maximum weekly growth was noticed during the autumn season (September to November) and a gradual decrease in weekly growth was observed during the winter season (December to February), where low temperature acts as a limiting factor for the growth of *A. yasumatsui* (Fig. 7). The climate of North and Central Florida is a humid subtropical one, whereas South Florida has a tropical climate. In this region, the highest weekly growth is during March and September, and the lowest growth is in May (Fig. 7).

Discussion

Here we show that most African countries have favorable climatic conditions for *A. yasumatsui* establishment under current climatic scenarios. These suitable areas closely overlap with the distribution of indigenous *Encephalartos* cycad species in Africa (Cousins and Witkowski 2017) (Fig. 1). *Aulacaspis yasumatsui* has the potential to spread quickly and threaten African cycad species (Emshousen et al. 2004, García et al. 2016). Our simulation indicates that with the change in climatic scenarios, many regions presently suitable become less suitable or unfavorable in the future (Figs. 3 and 4). This is largely driven by the predicted increase in temperature (Nakicenovic et al. 2000). These results are similar to the observations of Wei et al. (2018), but in our models, one can distinguish the extent of the suitability of a particular region for survival. In contrast, the increase in temperature also alters the insect lifecycle response with an increase in growth rate and development due to increased feeding rates (Battisti 2008). This type of response to climate change is observed in *A. yasumatsui*, and it is therefore expected to increases the number of generations it can complete in a year (Table 2). Similar trends of an increase in annual generations by herbivorous insects, such as the spruce web-spinning sawfly (*Ips typographus*) or green spruce aphid (*Elatobium abietinum*), to overcome the adverse effect of climate change has been observed elsewhere (Powell and Parry 1976, Ayres and Lombardero 2000, Battisti 2008, Netherer and Schopf 2010). Similar to *A. yasumatsui*, invasive species, such as the Argentine ant (*Linepithema humile*) or the giant African snail (*Achatina fulica*), have demonstrated a reduction of suitable habitat under a changing climate (Roura-Pascual et al.

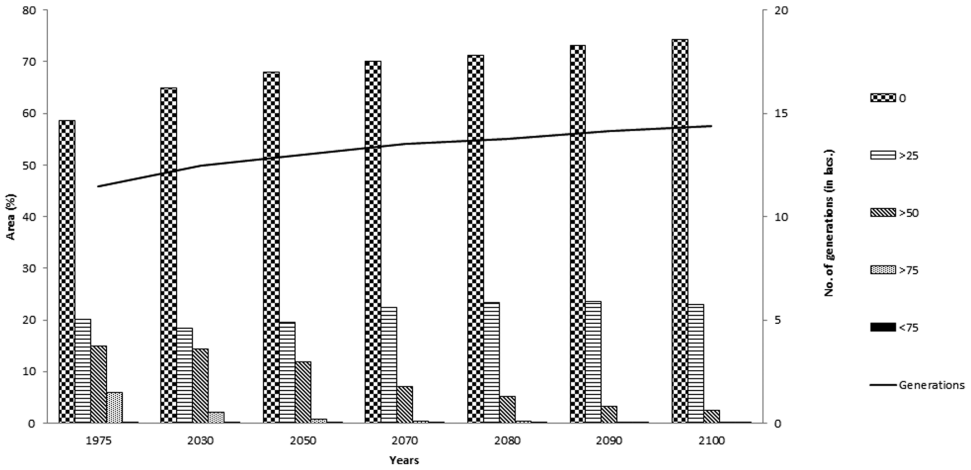

Fig. 5. Number of generations and percentage area suitability for *Aulacaspis yasumatsui* under climate change.

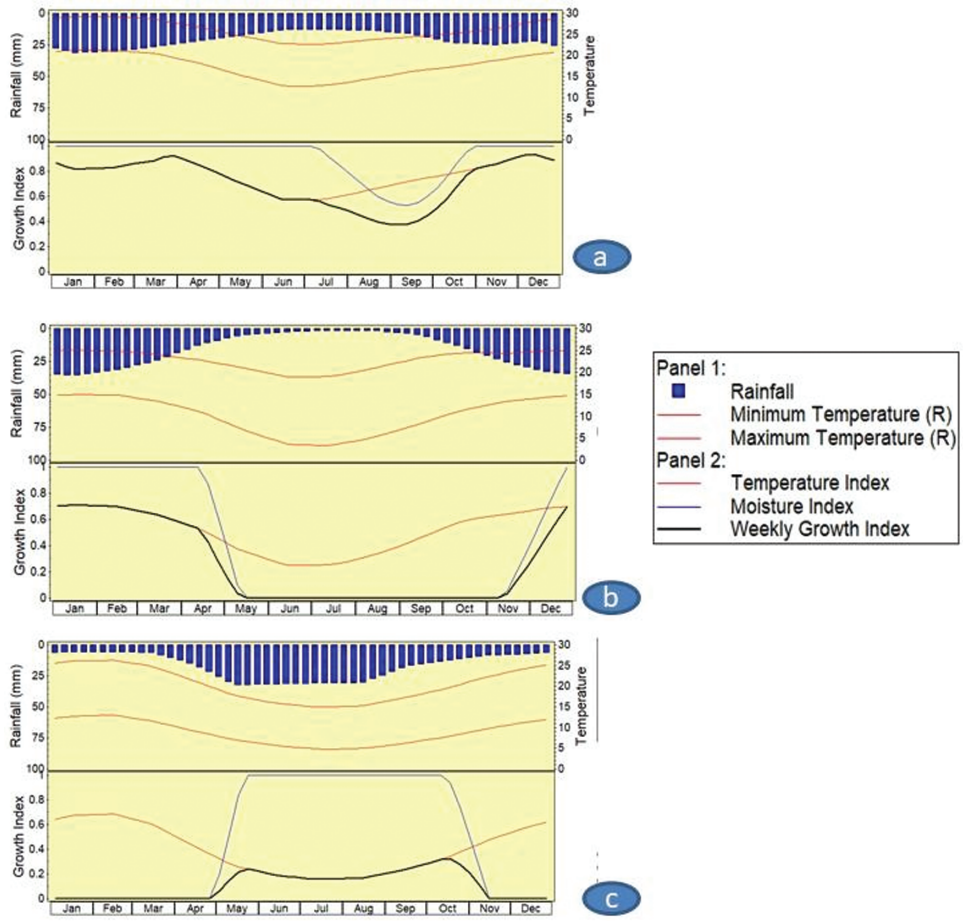

Fig. 6. Predicted growth index of *Aulacaspis yasumatsui* in three regions off South Africa (a) KwaZulu-Natal, (b) Limpopo, and (c) Western Cape.

2004, Sarma et al. 2015, Bradley et al. 2016). However, the prediction of potentially favorable regions can also be influenced by various other factors, namely, the dispersal ability of *A. yasumatsui* (Guisan and Thuiller 2005), host-plant availability in that particular region (Ning et al. 2017) and interspecific interactions (Gao and Reitz 2017). Interestingly, under increasing CO_2, the growth rate and leaf sugar content of *Encephalartos* increases linearly, which, in turn, might benefit insects such as *A. yasumatsui* feeding on cycad leaves (Nackley et al. 2017).

With *A. yasumatsui* present in South Africa (Nesamari et al. 2015) and potentially in Ivory Coast (Germain and Hodges 2007), there is an urgent need for strict quarantine measures across the

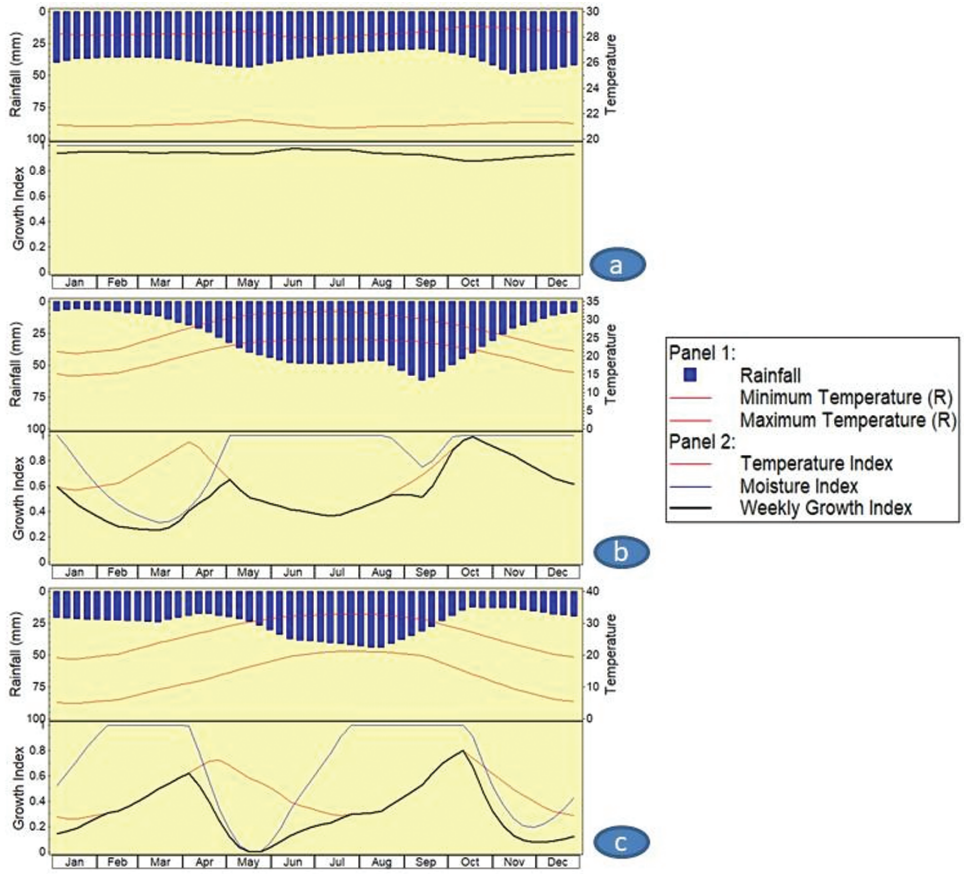

Fig. 7. Growth index of *Aulacaspis yasumatsui* in the native range and already established regions (a) Indonesia, (b) Taiwan, and (c) Florida.

borders of South Africa to prevent the *A. yasumatsui* invading neighboring countries like Zimbabwe and Mozambique that are also climatically suitable. From there, it could easily spread to central African countries, which all exhibit suitable climatic conditions and have endemic *Encephalartos* cycad species. Countries such as Congo, Gabon, Cameroon, and Liberia, with optimal climatic conditions (EI > 75) for the growth and survival of *A. yasumatsui*, should consider the risk of *A. yasumatsui* invasion and spread before they allow horticultural *Encephalartos* cycad import.

In South Africa, *A. yasumatsui* has localized distributions in Gauteng, KwaZulu-Natal, and Limpopo provinces (Nesamari et al. 2015). Our model showed that these regions also have the most suitable climate with EI values of <50 (suitable). Apart from these already invaded regions, other parts of South Africa, namely, parts of Western Cape, Eastern Cape, Free state, Mpumalanga, and Northwest provinces, also possess favorable climatic conditions for the establishment of *A. yasumatsui* (Fig. 2). This indicates the possibility of *A yasumatsui* occurrence in these regions, and field surveys might well be justified to identify and manage potential early infestations.

Studies by Cave et al. (2009) and Ravuiwasa et al. (2012) showed that the rise in temperature favored the growth of *A. yasumatsui*. Cycad grows well in abundant sunlight and adequate moisture conditions (Chamberlain 1919, Giddy 1974, Donaldson 1997). But, high soil moisture hinders the growth of cycads, which, in turn, can affect the growth of *A. yasumatsui* (William 1995). A similar trend in weekly GI was noticed in Indonesia, Taiwan, Florida regions, where *A. yasumatsui* is already established (Fig. 7). Furthermore, *A. yasumatsui* had the potential to survive in severe freezing conditions, as reported from Florida (Duke et al. 2003), suggesting that it is adaptable to harsh climatic conditions. Our predictions are in accordance with the previous studies on the population dynamics of *A. yasumatsui* in already invaded regions. Thus, making the developed CLIMEX model a reliable model to use for the potential distribution of *A. yasumatsui* in Africa under present and future climatic scenarios. Currently, there are no formal reports of highly damaging infestations of *A. yasumatsui* in Africa, but it cannot be ruled out in future, as *A. yasumatsui* has already caused severe damages to cycads in many other countries (Weissling et al. 1999, Heu et al. 2003, Malumphy and Marquart 2012).

Conclusion

Identifying those regions of Africa suitable for *A. yasumatsui* infestation and understanding the effect of climate change on *A. yasumatsui* survival is an important first step in management and for legislation. Out of the 54 African countries, 51 countries are at least partially suitable for *A. yasumatsui* establishment. With the change in climate, the majority of the central African nations—which are highly favorable for the establishment of *A. yasumatsui* in the current climatic scenario—will become gradually less favorable, but *A. yasumatsui* will still be able to establish. Therefore, prevention is key, and if already introduced, an early detection, rapid response approach should be followed. *Aulacaspis yasumatsui* control will benefit most using strategies that combine modification of cultural practices, biological as well as chemical

control following a developed Integrated Pest Management (IPM) plan. Additionally, our result suggests that to prevent further spread, close monitoring of cycads and strict quarantine measures should be implemented in areas where *A. yasumatsui* has not yet been recorded but where climate conditions appear to be suitable for establishment. Preventative legislation could aid in limiting the introduction. In South Africa, *A. yasumatsui* is currently categorized as a 'prohibited terrestrial invertebrate' in the invasive species legislation, National Environmental Management: Biodiversity Act, 2004 (NEM:BA). With *A. yasumatsui* naturalizing in South Africa and with many provinces possessing a favorable climate for growth and development and the potentially severe consequences for the many threatened cycad species, it warrants to be legislated and receive high priority from government-funded invasive species control programs.

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