



Climate change will likely facilitate invasion of Asian orchid *Eulophia graminea* into new areas

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Abstract Climate change plays an increasing role in the global biodiversity crisis. Alteration in local climatic conditions not only can negatively affect native biodiversity but also can accelerate the introduction and spread of invasive species. In this study the ecological niche modelling approach was used to evaluate possible changes in the distribution of suitable niches of invasive orchid *Eulophia graminea* within its native (Asia) and non-native geographical range (America, Australia). We mapped the current potential range of this species and analysed three various projections of future climate (for 2100) each with four different climate change scenarios (SSPs). Calculated niche overlap indexes indicated low similarity of niches occupied by native and invasive populations of *E. graminea* and Australian populations seem to be the most unique, while American and Asian groups share partially similar niches. The occurrence of the American population of *E. graminea* was correlated

especially with the temperature seasonality, while the Asian and Australian populations with annual precipitation and precipitation of the wettest quarter. As indicated in our analyses within Asia and America, *E. graminea* does not occupy all climatically suitable niches. On the other hand, in Australia the species studied already occupies all appropriate niche space. Climate change will likely be favorable for species studied to expand its range if the biotic components of its niche space (e.g., mycorrhizal fungi) will respond similarly. The most significant range expansion is predicted to occur in Australia which is interesting considering the marginally suitable habitats that *E. graminea* currently occupies.

Keywords Climate projection · Intercontinental invasion · Niche modelling · Shared socioeconomic pathways

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Introduction

Human activities are responsible for the accumulation of alien plant species across most regions of the world, a process that continues to this day (Seebens et al. 2017). Most of these species have been intentionally introduced for agriculture, forage, forestry, but most commonly as ornamentals (Beaury et al. 2021; Dodd et al. 2015; Rojas-Sandoval and Ackerman 2021). The latter pathway is particularly egregious as domestic gardens select species with traits

that are associated with invasion success (Guo et al. 2019). Unsurprisingly, many plants escape cultivation, spread into novel areas thereby becoming invasive with potential negative impacts on the environment, local biota, and human well-being (van Kleunen et al. 2018).

Non-indigenous plants, once introduced may become invasive without continued intervention by humans if environmental and biotic conditions are conducive for establishment and spread, even into undisturbed native vegetation (Mashhadi and Radosevich 2004) where they can be a major threat to native biodiversity and alter ecosystem functions (Lowry et al. 2012; Simberloff et al. 2013; Vitousek and Walker 1989). On the other hand, invasions may also create novel communities under human-impacted conditions that may provide ecosystem services such as soil conservation, nutrient cycling, wildlife habitat, carbon storage, watershed protection, and mitigate species extinctions (Lugo 2009). Whether or not the net outcome of biological invasions is negative, innocuous, or positive is likely context dependent, either environmentally, biologically, sociologically, or combinations of them all (Daehler 2003; Osborne and Gioria 2022).

Biological invasions are complex ecological processes which depend on propagule pressure, species invasive potential, and the susceptibility of communities to invasion (Chaffin et al. 2016; Chown et al. 2015; Lowry et al. 2012; Simberloff et al. 2013). Moreover, this process is currently accelerated by globalization which circumvents natural biogeographic barriers and increases propagule pressure, and accidental or intentional releases of non-native species (Hänfling and Kollmann 2002; Meyerson and Mooney 2007). Global warming can accelerate the spread of invasive species (Demertzis and Iliadis 2018) which can exacerbate climate change by increasing wetland methane and terrestrial nitrous oxide emissions (Bezabih Beyene et al. 2022).

Forecasting biological invasions is crucial for managing non-native species but any predictions of potential spread of exotics, should consider potential species niche shifts resulting from evolved environmental tolerances (fundamental niche) or the presence of novel conditions in the invaded range (realized niche) (Tingley et al. 2014). The niche shift in newly occupied regions (Rodder and Lotters 2009; Stiels et al. 2015; Zhu et al. 2017) can result from

fundamental niche shift (Müller-Schärer et al. 2004), release from dispersal barriers (Smith et al. 2020) or biotic constraints (realized niche shifts) (Mitchell et al. 2006). Also the spread of exotics is expected to be influenced by the physiological response of alien and native species to environmental changes and the subsequent changes in ecological interactions (Robinson et al. 2020).

Orchidaceae is the second largest family of flowering plants with more than 31,000 species (POWO 2023). Representatives of this group are found around the world, except polar regions and very dry deserts (Dressler 1981). Nonetheless, the highest orchid diversity is in the humid tropics (Vitt et al. 2023). Despite the great variation in morphology and physiology observed within Orchidaceae (Zhang et al. 2018), relatively few species are considered to be invasive or weedy (Ackerman 2007; Daehler 1998; Randall 2017).

In all biological invasions, there are barriers to overcome at every stage of an invasion (Blackburn et al. 2011). Major constraints to orchid establishment and spread involve symbioses. The first barrier is seed production. Fruit set in orchids is pollination limited, which is exacerbated by generally having one or very few pollinators (Ackerman et al. 2023; Tremblay et al. 2005). Although fruits can contain hundreds to millions of tiny, wind-dispersed seeds which to a certain extent compensates for low fruit set (Arditti and Ghani 2000; Sonkoly et al. 2016), dispersal is strongly leptokurtic and establishment is seed limited (Ackerman et al. 1996; Brzosko et al. 2017). Like most plants, orchids that have become invasive usually arrived at novel locations through the horticultural trade (Rojas-Sandoval and Ackerman 2021; van Kleunen et al. 2018), but subsequent stages of an invasion, establishment and spread, generally require seed production. If a novel location lacks a fauna that can provide pollinator services, then self-pollination and vegetative propagation are the only means for population growth and dispersal. Less than a quarter of orchid species have the capacity to autonomously self-pollinate (Ackerman et al. 2023), further constraining which orchids would be able to become established and spread.

The second hurdle to establishment success upon arriving at a novel location is the need to form an association with orchid mycorrhizal fungi (OMF). Orchid seeds are extremely small, lack endosperm

and are dependent on OMF to provide resources for successful germination (McCormick et al. 2018). Often this symbiosis is maintained into adulthood, although the OMF that provide for successful germination are not necessarily the same that associate with adult plants (Bayman et al. 2016; Phillips et al. 2020; Zhang et al. 2018). While some OMF have a very broad distribution, on a local scale they are not ubiquitous so that local orchid populations may associate with different sets of fungi that may involve niche and/or spatial segregation (Fernández et al. 2023; McCormick et al. 2018; Swift et al. 2019), although this is not always the case (Suarez et al. 2016). The spatial distribution of the fungi may be dependent on biophysical factors which, in turn, would affect the distribution of their orchid symbionts (Izuddin et al. 2019; Jacquemyn et al. 2016).

A rapidly spreading orchid species which is already present on several continents (Ackerman and González-Orellana 2021; Juárez Gutiérrez et al. 2023) is *Eulophia graminea* Lindl. (chinese crown orchid, grass leaved *Eulophia*). This terrestrial species is native to southern and central Asia. It produces rounded pseudobulbs and long, thin, linear leaves. The long inflorescence of *E. graminea* is composed of numerous flowers with greenish tepals and 3-lobed, white-pinkish lip. As summarized by Chang et al. (2010), there are several characters of *E. graminea* that likely facilitate its invasiveness. The quick germination and fast rhizome production enhance seedling survival and the short juvenile stage increases the expansive potential of this orchid. While pollinator availability is an important factor affecting long-term survival of most orchids, flowers of *E. graminea* are autogamous (Chang et al. 2010). Its dispersibility is exemplified by being one of the few orchid species to colonize remnants of Krakatau 25 years after the 1883 explosion (Partomihardjo 2003).

The first report of the chinese crown orchid outside its native range came from Australian Northern Territories (Macrae 2002; Pemberton 2013). Later it was recorded in South Africa (O'Conner et al. 2006) and USA (Pemberton et al. 2008). While the populations in Australia and Africa have not significantly spread since initial observations, its rapid range expansion in Florida has continued and has reached into the West Indies (Ackerman and González-Orellana 2021; Juárez Gutiérrez et al. 2023; Singhurst et al. 2020).

The reasons for the geographical differences in invasiveness are unknown.

The aim of this study is to evaluate differences in environmental niche preferences of *E. graminea* in various geographical regions, to visualize current non-native potential range of this orchid and to estimate the invasive potential of this species under various climate change scenarios using ecological niche modelling (ENM). Machine learning-based models are commonly used to estimate distribution of suitable niches of invasive species and predict their further spread in non-native areas (Cunze et al. 2020; Fand et al. 2020; Paclibar and Tadiosa 2019; Stiels et al. 2011).

Methods

List of localities

Localities of *E. graminea* were compiled from the Global Biodiversity Information Facility (GBIF 2022), herbarium specimens and field excursions. Only records which could be georeferenced with the precision of 1 km were used in ENM analyses and the duplicate presence records (records within the same grid cell) were removed using MaxEnt. The complete list of localities used in our study is available as Supplementary Table S1. Due to the lack of sufficient location data, the samples from South Africa were not included in further analyses.

Climatic niche similarity

We used a principal components analysis (PCA) to assess niche variability within the native and non-native distribution of *E. graminea* populations (from America, Asia and Australia). Each population was characterized by a set of 21 traits of which 19 were related to the climate data (Fick and Hijmans 2017), one described land cover (European Commission 2003), and one soil type (Hengl et al. 2017). To reduce bias, samples were spatially filtered at 5 km. Calculations were made with the software packages PAST ver. 4.03 (PAST PAleontological STatistics Version 3.20). The data matrix (Supplementary Table S2) was transformed (square root) before performing the ordination analysis.

Climatic niche modelling

The modelling of the current and future distribution of the species studied was done using the maximum entropy method implemented in MaxEnt version 3.3.2 (Elith et al. 2011; Phillips et al. 2006; Phillips and Dudik 2008), which is based on presence-only observations. Bioclimatic variables in 30 arc-seconds of interpolated climate surface downloaded from WorldClim v. 2.1 were used for the modelling (Fick and Hijmans 2017). The study area was divided into three geographical regions—America (0.15°S–44.16°N, 127.64–58.20°W), Asia (10.99°S–41.80°N, 67.54–159.78°E), and Australia (10.79–17.39°S, 125.98–138.09°E).

Pearsons' correlation coefficient was computed using SDMtoolbox 2.3 for ArcGIS (Brown 2014; Brown et al. 2017) (Supplementary Table S3) and highly correlated (>0.8) variables were removed from ENM analyses to prevent problems associated with auto-correlation. The final list of bioclimatic variables used in the analyses is provided in Table 1.

We predicted the future extent of *E. graminea* climatic niches for 2080–2100 by using four projections

for four Shared Socio-economic Pathways (SSPs): 1–2.6, 2–4.5, 3–7.0 and 5–8.5 (Li et al. 2021; McGee et al. 2000; Meinshausen et al. 2020). SSPs are trajectories adopted by the Intergovernmental Panel on Climate Change (IPCC), comprising narrative descriptions of future world development (Riahi et al. 2017). SSP storylines describe contrasting visions of future society and the assumed climate change challenges, with global warming in 2100 ranging from a low of 3.1 °C to a high of 5.1 °C above pre-industrial levels. O'Neill et al. (2017). Three different simulations of future climate developed by Coupled Model Intercomparison Project Phase 6 (CNRM), Goddard Institute for Space Studies (GISS), and Institute for Numerical Mathematics (INM) were used. We chose these projections because they present the most different simulations of maximum temperature and precipitation within study areas (Supplementary Figure S4).

In all analyses the maximum number of iterations was set to 10,000 and convergence threshold to 0.00001. The neutral (= 1) regularization multiplier value and auto features were used. The “random seed” option provided a random test partition and background subset for each run and 20% of the samples

Table 1 Climatic variables used in ENM analyses (marked with +)

Variable code	Variable description	Geographical region		
		America	Australia	Asia
bio1	Annual mean temperature	+	+	+
bio2	Mean diurnal range [mean of monthly (max temp–min temp)]	+	+	+
bio3	Isothermality (bio2/bio7) (× 100)	+	+	+
bio4	Temperature seasonality (standard deviation × 100)			
bio5	Max temperature of warmest month	+		
bio6	Min temperature of coldest month			
bio7	Temperature annual range (bio5–bio6)			
bio8	Mean temperature of wettest quarter	+	+	
bio9	Mean temperature of driest quarter		+	
bio10	Mean temperature of warmest quarter			
bio11	Mean temperature of coldest quarter			
bio12	Annual precipitation	+	+	+
bio13	Precipitation of wettest month			
bio14	Precipitation of driest month	+	+	+
bio15	Precipitation seasonality (coefficient of variation)	+	+	+
bio16	Precipitation of wettest quarter			
bio17	Precipitation of driest quarter		+	
bio18	Precipitation of warmest quarter	+	+	+
bio19	Precipitation of coldest quarter			

were used as test points. The run was performed as a bootstrap with 100 replicates. The output was set to logistic. We used the “fade by clamping” function in MaxEnt was used to prevent extrapolations outside the environmental range of the training data (Owens et al. 2013). All analyses of GIS data were carried out using ArcGIS 10.6 (Esri, Redlands, CA, USA). The evaluation of the created models was made using the area under the curve (AUC) (Mason and Graham 2002) and True Skill Statistic (TSS) (Čengić et al. 2020; Shabani et al. 2016).

To visualize changes in the distribution of suitable niches of the orchid, we used SDMtoolbox 2.3 for ArcGIS (Brown 2014; Brown et al. 2017). To compare the distribution model created for current climatic conditions with future predictions all SDMs were converted into binary rasters and projected using the Goode homolosine as a projection. The presence thresholds used in the analyses equaled the calculated minimum training presence threshold (Liu et al. 2005).

Based on obtained models the overlap of the climatic niches between the native and the introduced ranges was assessed using Schoener’s D and I statistics (Warren et al. 2008).

Results

Differences in occupied niches between geographical groups

The PCA analyses revealed the highest population density of *E. graminea* from America clustered in the center of the PCA plot, with distinct separate populations originating from Australia. Populations of the orchid from Asia were the most dispersed and occupied the right part of the PCA plot (Fig. 1). The analysis indicated that the first two principal components explained 73.8% of the total variance. The first component represented 41.1% of the total variance and the second component accounted for 32.7%. PC1 is correlated with bio16, bio12 and bio4. PC2 is correlated with bio14, bio16 and bio19. The first component demonstrates positive correlations with bio16 and bio12, and negative correlations with bio4. The second component demonstrates positive correlations with bio14 and bio19 (Supplementary Figure S5). The occurrence of the American population of *E. graminea* was correlated especially with bio4, while the Asian and Australian populations with bio16 and bio12.

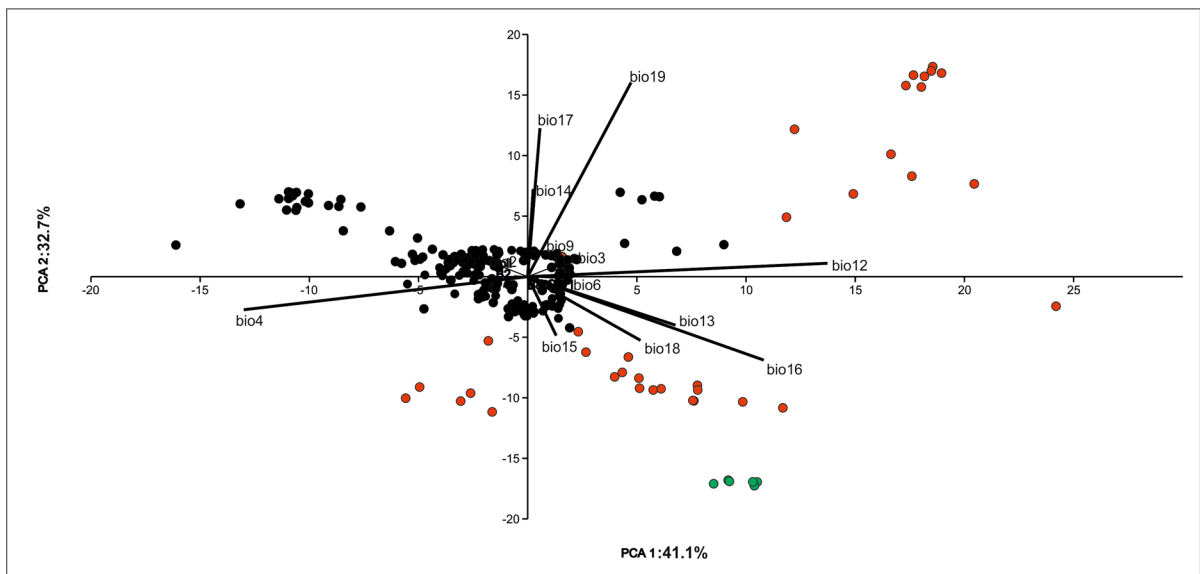


Fig. 1 PCA ordination diagram of studied localities of *Eulophia graminea* according to 21 environmental predictors (19 were related to the climate data, one described land cover and

one soil type). Legend: black dots—North American populations, red dots—Asian populations, green dots—Australian populations)

The sites occupied among geographical groups did not differ significantly in annual temperature (bio1) (Supplementary Figure S6); however, non-native populations seemed to be adapted to slightly higher temperatures (Asia 21.0–28.0 °C, America 23.0–35.0 °C, Australia 26.5–30.0 °C). The mean diurnal range of temperature (bio2) was narrower in American group (Asia 3–15 °C, America 3–8 °C, Australia 4–17.5 °C). Australian populations have narrower tolerance for isothermality (bio3; Asia—18–58, America 12–85, Australia 56–66). Considering annual precipitation (bio12) Australian populations are characterized by narrower tolerance for rainfall (Asia – 800 to 1800 mm, America – 1000 to 2000 mm, Australia 1700–2000 mm) and precipitation of the driest month (bio14; Asia 20–550 mm, America 50–550 mm, Australia – 0.5 to 6.5 mm). The precipitation seasonality (bio15) did not differ significantly among geographical groups (Asia 5–110, America 10–100, Australia 108–137), but precipitation of the warmest quarter was highly variable among regions (bio18; Asia 800–5800 mm, America 200–2000 mm, Australia 90–930 mm).

Calculated niche overlap indexes (Table 2) indicated low similarity of niches occupied by native and invasive populations of *E. graminea*. Australian populations seem to be the most unique, while American and Asian groups share partially similar niches.

Table 2 Niche overlap calculated using Schoener's D and I statistics

D/I	America	Asia	Australia
America	x	0.5919	0.0018
Asia	0.4670	x	0.0221
Australia	0.0002	0.0103	x

Table 3 Scores of model reliability tests and value of minimum training presence

Modelled area	AUC	TSS	Sensitivity	Specificity	Minimum training presence logistic threshold
America	0.986	0.959	0.977	0.982	0.0215
Asia	0.958	0.748	0.978	0.769	0.0295
Australia	0.999	0.9912	1	0.991	0.2174

Models evaluation and limiting factors

All created models received high scores of AUC (0.958–0.999) and mostly high scores of TSS (0.748–0.991) tests. Both sensitivity and specificity were also generally high indicating good reliability of presented modelling results (Table 3).

According to the jackknife test of variable importance, for both Asian and Australian populations bio12 (annual precipitation) was the variable with the highest gain when used in isolation, and the same variable decreased the most when it was omitted. Thus, it not only is the most informative, but also contains information not represented by the other variables. Models of American populations received different scores. The variable with highest gain when used in isolation was bio8 (mean temperature of the wettest quarter) while bio1 (annual mean temperature) decreased the gain the most when it was omitted (Supplementary Figure S5).

Current potential orchid range

Generally, current potential range of *E. graminea* is consistent with the known distribution of the species populations; nonetheless, Asian and American models indicated presence of suitable niches in some areas not occupied by this orchid (Fig. 2). Within Asian study area, suitable niches of *E. graminea* are located in New Guinea which is outside species known native range. In America, our model indicated Lesser Antilles, Jamaica, Dominica and Haiti as additional areas suitable for *E. graminea* occurrence. The Australian model is consistent with the distribution of known populations of the orchid.



Fig. 2 Current distribution of suitable niches of *E. graminea* in Asia (A), North America (B), and northern Australia (C)

Changes in the distribution of suitable niches of *E. graminea*

All analysed projections indicate that *E. graminea* will expand its native range in Asia (Table 4, Fig. 3); however, niches located currently in foothills of New Guinean Highlands, southern foothills of Müller mountains in Borneo, Indian Eastern Ghats will become unsuitable for the orchid. CNRM projections also indicate south-eastern Himalayan foothills, steppes and savannas of Myanmar as areas of potential range contraction for *E. graminea*. Expansion will mostly occur in south-western and south-central foothills of Himalayas, areas around Indian Chota Nagpur Plateau and Vindhya Range, Chinese Sichuan Plain, southern South Korea, and southern Honshu in Japan.

North American invasive populations will benefit from global warming and coverage of suitable niches of the orchid will expand for 36–193% (Table 4, Fig. 4), generally into the Great Plains, and north-eastern directions within US Coastal Plain. The range contraction is expected to occur (not in all scenarios) in Guatemala and Belize around the Belize River; Puerto Rico along the foothills of the Sierra de Cayey and Cordillera Central, and the Mogotes; Dominican Republic in lowlands north of Cordillera Central, south of the Cordillera Oriental, and the Cordillera Septentrional; Haiti along Massif du Nord and foothills of Massif de la Hotte; Jamaica primarily around Westmoreland and Saint Catherine parishes; Cuba along western foothills of the Sierra Cristal, western and northern foothills of Sierra Maestra (Supplementary Figure S7).

Australian populations of *E. graminea* will likely become extinct in GISS projection, but their potential invasive range will be larger than currently observed in both CNRM and INM simulations. In the latter

two predictions the coverage of suitable niches of *E. graminea* will be several times larger than currently recorded (Table 4, Fig. 5). In these scenarios species will expand its range in Melville and Bathursts islands, and south from Darwin to West Daly region. In some scenarios additional niches will also become available for *E. graminea* around the South Alligator River estuary.

Discussion

Potential versus observed geographical range

Every species has a fundamental niche of which only a portion is occupied (realized niche). The elements constituting both types of niche cannot be completely described but can be estimated as a hypervolume of various biophysical parameters (Blonder et al. 2014). During the expansion into non-native geographical regions invasive species generally occupy the same hypervolume constituted by the fundamental niche of the species as defined by its native range (Aravind et al. 2022).

As indicated in our analyses even within Asia, *E. graminea* does not occupy all climatically suitable niches. That may be caused either by geographical barriers preventing spread, unmeasured natural or human-induced abiotic conditions (Wraith et al. 2020), or by constraining biotic factors in unoccupied areas, e.g. lack of symbiotic mycorrhizal fungi (Downing et al. 2020), presence of herbivores and pathogens (Meena et al. 2018; Meena and Mani 2022). However, it should be noted that the actual sensibility of natural orchid populations to pathogens is still little recognized (Melendez and Ackerman 1993). A similar situation of uninhabited

Table 4 Changes in the coverage (km²) of the suitable niches of *E. graminea*

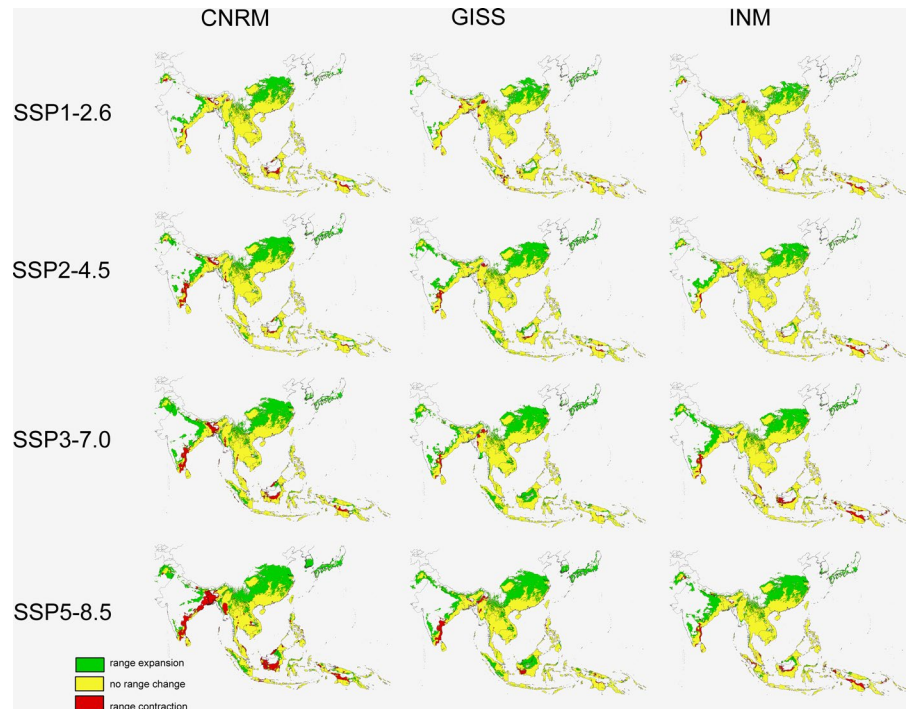
Geographical region	Projection	SSP scenario	Range expansion	No range change	Range contraction	Change (%)
North America	CNRM	1–2.6	503,775.4	576,167.5	27,525.28	+79
		2–4.5	770,379.3	582,260.7	21,432.05	+124
		3–7.0	882,609.6	476,440.1	127,252.6	+125
		5–8.5	1,295,440	470,612.6	133,080.1	+193
	GISS	1–2.6	444,069.4	544,644.5	59,048.22	+64
		2–4.5	456,440.7	543,423.5	60,269.27	+66
		3–7.0	580,439.4	528,220.5	75,472.24	+84
		5–8.5	526,820.6	484,518	119,174.7	+68
	INM	1–2.6	264,659.7	556,143.1	47,549.68	+36
		2–4.5	366,845.5	546,330.8	57,361.96	+51
		3–7.0	722,937.2	561,093.5	42,599.26	+113
		5–8.5	929,173.8	569,635.7	34,057.05	+148
Asia	CNRM	1–2.6	1,591,586	5,189,896	328,331.2	+23
		2–4.5	2,059,589	5,150,549	367,678.3	+31
		3–7.0	2,415,786	4,936,159	582,068.7	+33
		5–8.5	2,645,666	4,403,998	1,114,230	+28
	GISS	1–2.6	1,286,665	5,206,398	311,829.6	+18
		2–4.5	2,058,696	5,307,062	211,165.9	+33
		3–7.0	2,463,861	5,351,687	166,540.4	+42
		5–8.5	2,688,171	5,150,799	367,428.1	+42
	INM	1–2.6	988,160.4	5,203,643	314,584.9	+12
		2–4.5	1,479,287	5,274,574	243,653.5	+22
		3–7.0	1,943,816	5,056,149	462,078.8	+27
		5–8.5	2,182,075	5,137,480	380,747.9	+33
Australia	CNRM	1–2.6	1975.163	503.5561	564.6961	+132
		2–4.5	13,809.15	1068.252	0	+1293
		3–7.0	7569.475	977.3913	90.86087	+700
		5–8.5	7622.123	701.412	366.8402	+679
	GISS	1–2.6	0	0	1068.252	–100
		2–4.5	0	0	1068.252	–100
		3–7.0	0	0.849167	1067.403	–100
		5–8.5	0	71.33003	996.9221	–93
	INM	1–2.6	8646.219	838.977	229.2751	+788
		2–4.5	7750.348	1068.252	0	+726
		3–7.0	2418.428	990.1288	78.12337	+219
		5–8.5	855.1112	723.4903	344.7618	+48

potential range is observed in North America; however, because unfilled niches are located on islands, time and geographical barriers are most probable reasons for unoccupied but potentially suitable areas in this region. Time is a factor as this invasion is relatively recent having been first noted in 2007 and new populations are discovered every year. We have anecdotal evidence that stratified dispersal is likely

involved: long-distance dispersal to islands from Florida (USA) via the landscape trade in topsoil and potted plants; and local wind-dispersal of the dust-like seeds.

In Australia the species is not expected to spread under current conditions since it already occupies all appropriate niche space which is only marginally suitable based on our analyses of its native range. In

Fig. 3 Changes in the distribution of suitable niches of *E. graminea* in Asia in various climate change scenarios



comparison, American and Asian groups are more similar to each other, but still the overlap in occupied niches between these regions is low.

Impact of global warming.

Climate change can accelerate non-native plant invasions by altering environmental conditions, which may shift the geographical distribution of suitable niche components and affect normal regimes of habitat disturbance (e.g., the frequency, duration, and severity of climatic events). Further change may occur through human responses to these changes (Adhikari et al. 2019; Blumenthal et al. 2013; Dukes and Mooney 1999; Turbelin and Catford 2021).

Climate change will likely be favorable for *E. graminea* to expand its range if the unaccounted biotic components of its niche space (e.g., mycorrhizal fungi) will respond similarly. The most significant range expansion is predicted to occur in Australia (in 2 of 3 projections) which is interesting considering the marginally suitable habitats that it currently occupies.

Orchids are generally not considered to be harmful where they have invaded. However, a study conducted in Puerto Rico demonstrated apparent competition between mixed populations of introduced *Spathoglottis plicata* on a native orchid, *Bletia patula*

(Recart et al. 2013). The invasive orchid was the preferred host of a native, orchid specialist weevil, *Stethobaris polita*, previously regarded as a relatively rare beetle. Flower and fruit damage to *S. plicata* was high with significant demographic consequences, but population growth rates remained positive (Falcón et al. 2017). Elevated beetle populations resulted in increased weevil attack on the native orchid, significantly reducing fruit production. Two other common, non-indigenous orchids on the island also serve as hosts, *Arundina graminifolia* and *Dendrobium crumenatum*, and may elevate weevil populations as well, with possible impacts on native species (Foster and Ackerman 2021). The other orchid which is considered by local authorities to constitute a threat to native plants is *Disa bracteata* which invaded Australia in 1944 (Wapstra et al. 2020). However, in this case there is no evidence of negative effects on the Australian flora. We are unaware of any studies designed to detect the consequences of *E. graminea* invasions.

The two most obvious ecological constraints for any orchid species persistence are (1) availability of pollen vectors and (2) presence of microbial symbionts in the environment. The former is not likely a problem for *E. graminea* since the flowers appear

Fig. 4 Changes in the distribution of suitable niches of *E. graminea* in North America in various climate change scenarios

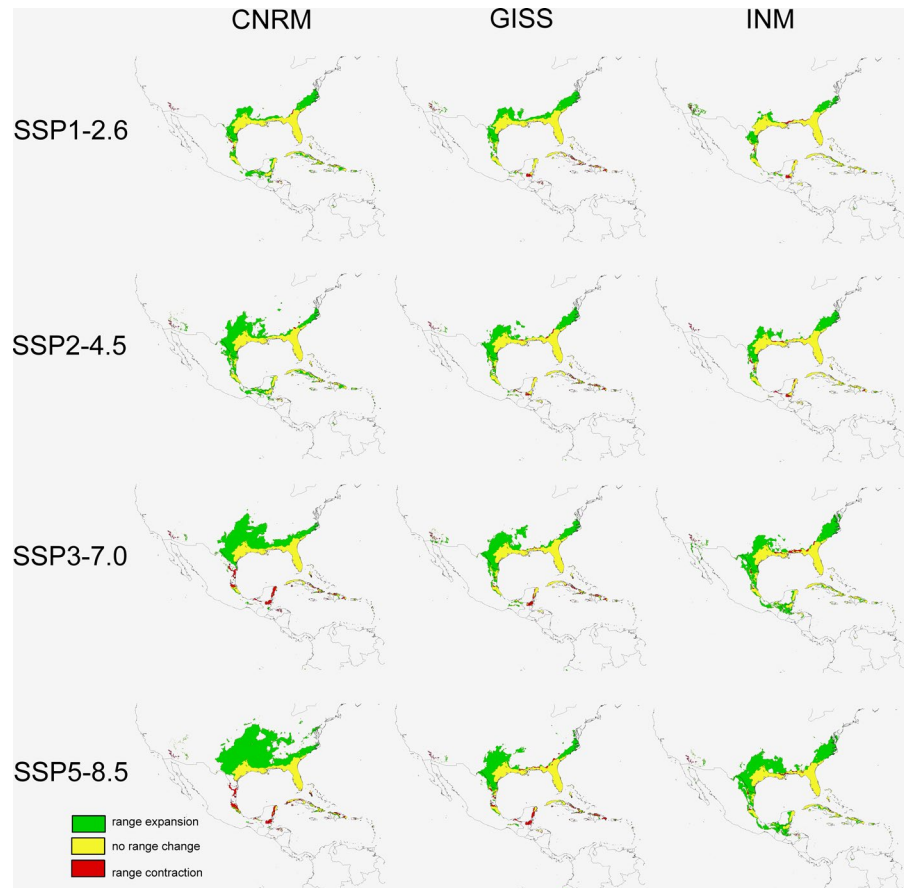
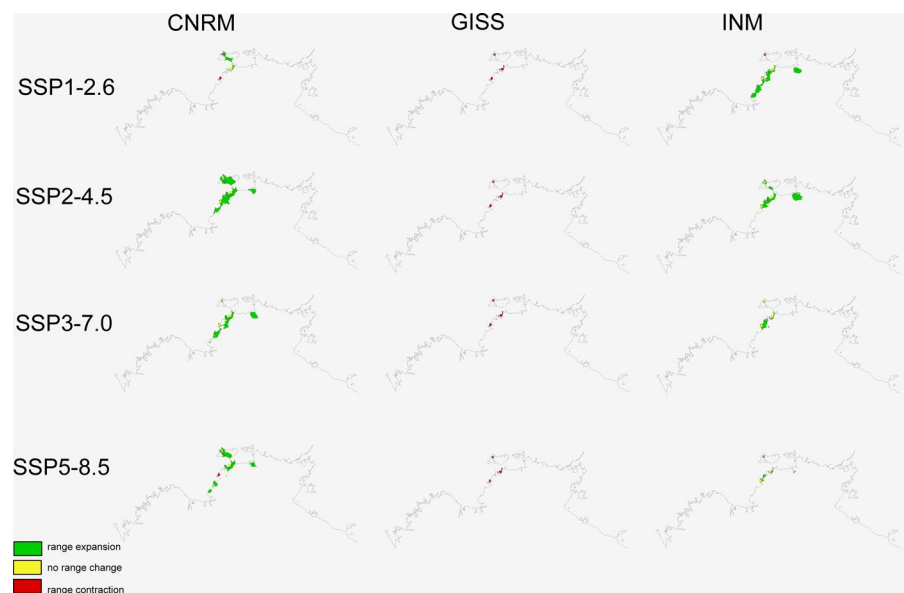


Fig. 5 Changes in the distribution of suitable niches of *E. graminea* in Australia in various climate change scenarios



to be self-pollinating, perhaps by the same mechanism as *E. maculata* (Chang et al. 2010; González-Díaz and Ackerman 1988). The flowers contain small quantities of nectar (0.5 µl; (Ackerman and González-Orellana 2021) so the potential for a mutualistic plant-pollinator interaction exists, but thus far no pollinators have been reported (Ackerman et al. 2023). On the other hand, *E. graminea* cannot escape the need for OMF. Based on expectations of bipartite networks, invasive or widespread native orchids likely specialize on a widespread OMF, or be a generalist in the number of OMF that they can exploit (Ackerman 2007; Bascompte et al. 2003; Vázquez and Aizen 2004). Downing et al. (Downing et al. 2020) compared the OMF of *E. graminea* from its native range in southwest China and the OMF of the species in its invasive range (Florida, USA) and concluded that *E. graminea* is a generalist with respect to its OMF as 10 of 18 fungal strains tested had successfully germinated seeds ex situ. The OMF are known for only two other invasive orchids, *Eulophia* (as *Oeceoclades*) *maculata* and *Disa bracteata* and both orchids associate with widespread OMF (Bayman et al. 2016; Bonnardeaux et al. 2007). While broad-scale analyses across the geographical regions are needed to uncover the importance of fungal partner(s) for orchid long-term survival, current results suggest that availability of OMF may not be a constraint to any of these invasive orchids now or in the future under climate change scenarios. Nonetheless, the orchid and its OMF symbionts will not necessarily respond to climate change similarly (Kolanowska 2023). Although OMF have garnered most of the attention because of their importance in seed germination, other microbial endophytes can have fitness consequences by affecting plant growth, resistance to pathogens, and tolerance capacity to biotic and abiotic stresses. We know very little about these interactions in an ecological or biogeographical context (Bayman et al. 2002; Saraiya et al. 2019).

Model deficiencies

This study, as any other simulation, has its limitations. The models of future distribution of suitable niches of *E. graminea* are based exclusively on the climatic data. The grass leaved *Eulophia* is a terrestrial species and depends on the soil properties which may also be altered by climate changes.

However, currently it is not possible to evaluate the possible alterations in the soil physical, chemical or biotic properties resulting from global warming. According to our data (Supplementary Table S2) *E. graminea* can grow in eleven different soil types (acrisols, arenosols, cambisols, ferralsols, fluvisols, gleysols, histosols, leptosols, luvisols, phaeozems, vertisols) and apparently has rather broad tolerance for various substrates.

The other factor which was not included in our analyses was geographical distribution of mating system. We only know that flowers of native Taiwan populations are autogamous (Chang et al. 2010), but in other regions, native or non-native, reproduction in *E. graminea* may be pollinator-dependent. This may be important because orchid species and their pollinators will not necessarily respond to climate change in the same manner so potential range shifts of both should be assessed (Kolanowska 2021; Kolanowska et al. 2021).

Some orchids are characterized by very specialized relationships with mycorrhizal partners and for these species predictions of future distribution should be accompanied with the analyses of changes in the potential ranges of their symbionts (Kolanowska 2023). Unfortunately, little is known of the endophytic biota of *E. graminea* (Downing et al. 2020) and even less of their geographical distribution so ENM of the ecological relationships of this species was not possible.

Obviously, considering human impact on *E. graminea*, the most damaging is direct habitat destruction which cannot be predicted and included in simulations. However, the ecological amplitude of this orchid is remarkable. It grows in sandy beaches, coastal grasslands, lowland shrubs and open forests. It also does very well in lawns, roadsides, parks, home and hotel gardens (Ackerman and González-Orellana 2021; Chang et al. 2010). This broad tolerance and ability to adapt to various environments constitutes an advantage of *E. graminea* in human-altered ecosystems.

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Data availability The datasets analyzed during the current study are available as supplementary information.

Declarations

Conflict of interest The authors declare that they have no financial or non-financial conflicts of interest.

Consent for publication All authors provide their consent for publication.

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