Climatic niche shift and possible future spread of the invasive South African Orchid *Disa bracteata* in Australia and adjacent areas (#26096)

First revision

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Climatic niche shift and possible future spread of the invasive South African Orchid *Disa bracteata* in Australia and adjacent areas

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Orchids are generally regarded as plants with an insignificant invasive potential and so far only one species has proved to be harmful for native flora. However, previous studies on *Epipactis helleborine* and *Arundina graminifolia* indicate that the ecological aspects of range extension in their non-native geographical range is not the same for all species of orchids. *Disa bracteata* in its native range, South Africa, is categorized as of little concern in terms of conservation whereas in Australia it is naturalized and considered to be an environmental weed. The aim of this research was to determine the ecological preferences enabling the spread of *Disa bracteata* in Western and South Australia, Victoria and Tasmania and to evaluate the effect of future climate change on its potential range. The ecological niche modelling approach indicate that most of the accessible areas are already occupied by this species but future expansion will continue based on four climate change scenarios (rcp26, rcp45, rcp60, rcp85). Further expansion is predicted especially in eastern Australia and eastern Tasmania. Moreover, there are some unpopulated but suitable habitats in New Zealand, which according to climate change scenarios will become even more suitable in the future. The most striking result of this study is the significant difference between the conditions recorded in the areas it naturally inhabits and invasive populations that indicate a possible niche shift. This species in Australia currently continues to populate a new niche or exploit habitats that are only moderately represented in South Africa.

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Abstract

Orchids are generally regarded as plants with an insignificant invasive potential and so far only one species has proved to be harmful for native flora. However, previous studies on *Epipactis helleborine* and *Arundina graminifolia* indicate that the ecological aspects of range extension in their non-native geographical range is not the same for all species of orchids. *Disa bracteata* in its native range, South Africa, is categorized as of little concern in terms of conservation whereas in Australia it is naturalized and considered to be an environmental weed. The aim of this research was to determine the ecological preferences enabling the spread of *Disa bracteata* in Western and South Australia, Victoria and Tasmania and to evaluate the effect of future climate change on its potential range. The ecological niche modelling approach indicate that most of the accessible areas are already occupied by this species but future expansion will continue based on four climate change scenarios (rcp26, rcp45, rcp60, rcp85). Further expansion is predicted especially in eastern Australia and eastern Tasmania. Moreover, there are some unpopulated but suitable habitats in New Zealand, which according to climate change scenarios will become even more suitable in the future. The most striking result of this study is the significant difference between the conditions recorded in the areas it naturally inhabits and invasive populations that indicate a possible niche shift. This species in Australia currently continues to populate a new niche or exploit habitats that are only moderately represented in South Africa.

Introduction

The study of biological invasions has been called “one of the hottest current topics in ecology” (Sol 2001), mostly because together with habitat destruction and climate change the spread of non-native organisms is considered to be a major threat to biodiversity. In Australasia, invasive (= not native) species are a major problem, for example, the number of species of plants reported as introduced, that have been released and may or may not have become naturalized in Australia exceeds 28,000 (Randall 2007). A subset of them have naturalized and are a threat to the rich endemic flora of that continent (Coutts-Smith & Downey 2006, Randall 2007, Duursma, et al. 2013) as the populations are self-sustaining and spreading without human assistance. In addition, the eradication of exotic weeds is costly (Sinden et al. 2004). Governmental agencies and private landowners invest large amounts of money in controlling the spread of ~~certain~~ species and use various methods ~~to assess risk~~. One widely used technique is to predict the potential future ranges of invasive species using climatic niche modelling (Peterson 2003).

~~In the present paper~~, we use this approach to study the invasive orchid species, *Disa bracteata* Sw., which was first reported in Australia ~~relatively recently, in the mid-XX century~~. It is listed in the Global Compendium of Weeds (GCW; http://www.hear.org/gcw) and is the only weedy representative of the mainly sub-Saharan genus *Disa* P.J. *Disa bracteata* is classified in the GCW as an environmental weed (species that invade native ecosystems; Blood 2001) or a naturalized species (self-sustaining and spreading populations but not necessarily effecting the environment; Baker et al. 2005; Hussey et al. 1997). *D. bracteata* is a South African endemic found in both the Eastern and Western Cape (Foden & Potter 2005), where it is widespread and common, especially in areas subject to mild disturbance. In undisturbed vegetation it is somewhat less frequent. *D. bracteata* is included on the Red List of South African plants as a taxon of Least Concern (Raimondo et al. 2009; Foden & Potter 2005). In the mid-20th-century it was brought to Australia where along with another 2700 non-native species of plants it became naturalized (Groves et al. 2003). This orchid was first formally recorded near Bacchus Marsh, west of Melbourne, in 1944 (Wileman 2015, Russell 2015) and ~~more numerously~~ since 1945 in areas of the Great Southern Region in Western Australia (vicinity of Albany). Later it was also recorded in South Australia in 1988 and Victoria in 1994. Recently it was reported in Tasmania (Gullan, Viridans Biological Databases). In Australia *D. bracteata* was probably accidentally introduced and is now growing along roadsides. Invasive populations are large with up to almost 80 mature individuals in one square meter (Tucker 2006, Trees For Life).

The aim of this research was to evaluate the similarities in the ecological niches occupied by invasive and native populations of *D. bracteata* and estimate the potential further spread of this species in Australia and adjacent areas. The comparison of its climatic preferences in Africa and in Australia over time would help in explaining the nature of its invasion by providing information about the early and current stage of spread of *D. bracteata*. Currently it is unclear whether this orchid occupies similar niches in Australia and Africa or was able to invade new niches in Australia. While exotic orchids have previously not been considered to negatively affect native flora, we do believe that our analyses of possible future spread of *D. bracteata* will be useful for conservation purposes.

Materials and methods

Localities

A database of localities of *D. bracteata* was prepared based on the information recorded on the labels of identified herbarium specimens deposited in MO, WAG, S, NY, AD, MEL, CANB, HO, NSW and PERTH. The herbaria acronyms follow *Index Herbariorum* (Thiers 2015). The process of georeferencing follows Hijmans et al. (1999). The geographic coordinates provided on the herbarium sheet labels were verified. If there was no geolocation data on the herbarium sheet label, the description of the collection place recorded was assigned coordinates as precisely as possible. In addition, the information provided by the South African National Biodiversity Institute and Global Biodiversity Information Facility (GBIF) with a precision of greater than 1000 m was used. A total of 187 native and 747 invasive records were gathered (Supplementary file 1).

Niche modelling

Nineteen bioclimatic variables from the CHELSA version 1.1 database (Karger et al., 2016, Karger et al., 2016) were used. ~~The recent study of~~ Bobrowski & Schickhoff (2017) indicates that this dataset performs better than other available climatic data in ecological niche modelling. Eighteen soil characters relevant to plant growth were obtained from Global Soil Information Based on Automated Mapping (Hengl et al. 2014; www.soilgrids.org) with a 250 m^2 resolution and upscaled to match the resolution and extent of the bioclimatic variables. In addition, other georeferenced factors were used in the analyses: potential vegetation (Ramankutty & Foley 1999), soil quality (Fischer et al. 2008) along with six topographic variables based on an altitude raster (Supplementary file 2). All maps were clipped using a rectangular mask enclosing known populations and surrounding regions in order to estimate possible migration and/or spread. Since this species continues to spread mainly in Australia the northern border of the Australian continent was set as the maximum extent of spread in this study. To account for ~~the~~ co-linearity and select the most important bioclimatic variables, the number of original bioclimatic data was reduced using the R package MaxentVariableSelection (Jueterbock 2016) ~~and applying the~~ following criteria: correlation threshold was set at 0.7, contribution threshold at 1 and beta-multiplayer was tested in the range of 1 to 15 using 0.5 steps and in the range of 1 to 1.5 using 0.1 steps.

The modelling was done using the maximum entropy method implemented in Maxent version 3.3.3k (Phillips et al. 2004), which is commonly used in ecological studies and is known to be reliable (Kolanowska and Konowalik 2014, and references therein). The maximum number of iterations was set at 10^4 and convergence threshold at 10^{-5}. For each run, 20% of the data was used and set aside as test points. The "random seed" option, which provides a random test partition and background subset for each run was used. The run was performed as a bootstrap with 10^3 replicates and the output was set to cumulative.

To evaluate the possible future expansion of *D. bracteata* within Australia, climate projections obtained from Coupled Model Intercomparison Project Phase 5 (CMIPP5) were used. Four "representative concentration pathways" (RCPs: rcp26, rcp45, rcp60, rcp85), which differ in predicted CO_2 concentration (IPCC 2013), were analyzed. We only considered the models covering all four representative concentration pathways for the year 2070 (average for 2061-2080). These models were obtained from www.worldclim.org (Supplementary file 2). To reduce the bias caused by the selection of only one specific model, they were averaged and the ensemble map for each variable, in particular RCP, was computed (Konowalik et al. 2017). This step simplifies the interpretation as it shows the general trend specific for a given RCP scenario while reducing extremes and uncertainties of particular models. Since many soil variables may be potentially affected by climate warming and due to the absence of such models for the region studied they were not used for future predictions. For the presentation of results, output grids with a cumulative scale were converted to binary grids using maximum training sensitivity plus a specificity threshold (Liu et al. 2005, Liu et al. 2016).

A range of methods described in previous studies (Kolanowska and Konowalik 2014) was used to analyze output from niche modelling and quantify differences between indigenous and invasive populations. Niche equivalency ~~test~~ (Warren et al. 2008) was calculated using ‘ENMTools’ R package (Warren 2016). Niche overlaps (D and I) were calculated using methods of Warren et al. (2008) and Broennimann et al. (2012). Schoener's D statistic uses direct measures of species density, which in this study ~~are~~ changed to measures of densities of occurrence modelled in environmental space. `I' statistic ~~is~~ based on the modified Hellinger distance that compares two probability distributions. These two metrics range from 0 (no similarity) to 1 (high similarity). The bias metric (Pressey et al. 2000) was calculated as described previously (Kolanowska and Konowalik 2014). Principal Component Analysis (PCA) was performed on all available variables (Appendix 3), as described in Kolanowska and Konowalik (2014) using R (R Core Team 2016). All GIS operations were done in open source software QGis (Quantum GIS Development Team 2016) and R (R Core Team 2016) using packages ‘raster’ (Hijmans 2016) and ‘rgdal’ (Bivand et al. 2016).

Results

Variable selection and model evaluation

According to MaxentVariableSelection (Jueterbock 2015), the lowest AIC, AICc, BIC scores and highest AUC for training dataset are assigned to the model with beta-multiplayer = 1. The final set of the most important and uncorrelated variables included eight of the original 49 variables: Temperature Annual Range (Bio7), Mean Temperature in Wettest Quarter (Bio8), Precipitation Seasonality (Bio15), Precipitation in Warmest Quarter (Bio18), Precipitation in Coldest Quarter (Bio19), Sand Content, Soil Organic Carbon Content, Soil pH.

The calculated value of the area under the curve (AUC) was 0.98 (SD 0.001), which indicates ~~an~~ excellent model performance. Additional summary statistics ~~were calculated,~~ the mean crossentropy (mxe), which equaled 0.019 (SD 0.001), and root-mean-squared error (RMSE), which was 0.073 (SD 0.002). Both of these values are very low, which indicate ~~a~~ good performance ~~of the model.~~

Potential distribution of suitable niches under current climatic conditions

The model of the current distribution of suitable niches for *D. bracteata* was calculated based on all uncorrelated variables and a model in which climatic factors were considered exclusively are rather congruent (Fig. 1 A and B, Fig. 2 A and B). The main difference concerns the transitional zone between the western and eastern Cape in Africa, and the Nullarbor Plain in Australia. The first region was not indicated as suitable in the model based on climatic factors, whereas the second one was shown as suitable for this orchid in this analysis. Otherwise the difference may be ~~also~~ seen in the scale of suitable habitat – while the general trend is very similar both models differ slightly in the extent of the predicted suitable niche. Currently, the species is found in most of the suitable habitats in both Africa and Australia. Yet there are some areas in Australia that are not colonized - the Eyre Peninsula and some smaller areas detached from the main distribution. A vast area of Tasmania is predicted to be suitable but so far the occurrence of *D. bracteata* ~~is~~ reported only from the northern part of the island. Also, there are no records of this orchid from New Zealand (especially the North and South Islands) although the models indicate the existence of suitable habitat in this area.

Future changes in the extent of suitable habitat

Future climate scenarios indicate that the extent of the ~~environmentally suitable~~ niche in South Africa will be very similar to the one observed today. Nevertheless, depending on the climate change scenario used the extent of ~~suitable habitat~~ can slightly decrease or increase. Two models (rcp26 and rcp60) predict that suitable niches for *D. bracteata* will become available along the Atlantic coast, near the border of Namibia and South Africa, in areas around northern Namaqualand, Sperrgebiet and Lüderitz Bay (Figure 1: C and E).

Within the invasive range, all models indicate that additiona~~ly~~ suitable niches could occur in New Zealand, especially along the southern coast of North Island and South-eastern coast of South Island. Simultaneously, all scenarios predict ~~the loss of habitat~~ in Western Australia, especially in the area north of Leeuwin–Naturaliste Ridge.

Apart from these general trends, each of the future climate scenarios gave specific information on the future potential range of *D. bracteata*. The Rcp26 scenario prediction is that more suitable habitats will be located in the south-western and south-eastern part of the Great Dividing Range, south-central and south-eastern part of the Nullarbor Plain, and in the northern part of New South Wales (Fig. 2C). Scenario rcp45 indicates a potential ~~extension~~ of range in south-western and south-eastern part of the Great Dividing Range and south-western part of the Nullarbor Plain (Fig. 2D). Scenario rcp60, like the first scenario, predicts the occurrence of ~~more suitable habitats~~ in the south-western and south-eastern part of the Great Dividing Range, south-central and south-western part of Nullarbor Plain and in the northern part of New South Wales (Fig. 2E). Rcp85 scenario indicates that *D. bracteata* may spread in the south-western part of the Great Dividing Range and south-central and south-eastern part of Nullarbor Plain (Fig. 2F).

Niche overlap and identity

The overlap between the ~~ecological~~ requirements of invasive and the natural populations is moderate or even low. Statistics calculated according to Broennimann et al. (2012) are D = 0.35 and I = 0.58. These values were slightly higher using the method of Warren et al. (2008): D = 0.44, and I = 0.73. Also, niche identity tests reveal that the niches occupied by invasive and natural populations are different ($p < 0.01$). Visualization using PCA (Figure 3) indicates a large overlap between the niches and only a small proportion of which is different.

Environmental conditions recorded at the sites occupied by this species are illustrated in Figure 4. To illustrate the dissimilarity between invasive and native populations a bias metric was calculated. It indicates that all invasive populations occupy relatively different habitats compared to populations in Africa (Chi-squared = 46.031, $p = 4.9 \times 10^{-4}$). The same result is obtained when the invasive records are considered as one dataset or when the records are divided into those for Eastern and Western Australia (Chi-squared = 73.807, $p = 4.9 \times 10^{-4}$). Nevertheless, the suitable niches of both groups of Australian populations are also different (Table 1). There are, however, two similarities in the ecological characteristics of these two Australian regions: there is a greater sand content and lower precipitation in the warmest quarter in the areas occupied relative to that in areas occupied by natural populations. Others have either a medium difference (e.g. soil pH) or a significant dissimilarity (e.g. temperature annual range, mean temperature in wettest quarter, precipitation seasonality, precipitation in coldest quarter and soil organic carbon content; Table 1).

Discussion

Orchids are not usually regarded as weeds although some, e.g. *Epipactis atrorubens*, *E. helleborine* and *Dactylorhiza majalis*, colonize secondary habitats in temperate Europe (Adamowski 2006, Rewicz et al. 2015). Even fewer species are reported as invasive (e.g. Ackerman 2007) and so far only one, *Spathoglottis plicata*, has been shown to negatively affect native plants (Recart et al. 2013).

The invasive success of *D. bracteata* has not been thoroughly investigated and the mechanisms of this phenomenon remain unclear. The only predictive models are in Weed Futures (www.weedfutures.net; Duursma et al. 2013). Most ground orchids usually do not have great potential for spreading because of their very specific ecological requirements. ~~In addition to the ordinary factors limiting the distribution of plants, such as soil properties and climate,~~ Orchidaceae often have specific insect pollinators and ~~a particular fungal species~~ that needs to be present in the soil to enable seed germination (e.g. Batty et al. 2002, Cozzolino and Widmer 2005, McCormick and Jacquemyn 2014).

Many species of orchids will only germinate with the aid of one or a few species of fungus so their distribution, and hence ecological success, is heavily dependent on suitable conditions for the fungus. *Disa bracteata* appears to be able to form an association with a large number of fungal partners, especially those that can survive in disturbed soils (Bonnardeaux et al. 2007), thus it is much less limited in terms of the places and conditions in which it may become established. For this reason, we did not incorporate the distribution of mycorrhizal fungi in our analyses. It is noteworthy that the incorporation of a fungal factor in any analysis of orchid distribution is extremely difficult. Most orchid mycorrhizal fungi belong to the genus *Rhizoctonia*, a diverse polyphyletic group that are difficult to classify and molecular methods have become the standard means of assigning these orchid fungi to groups within the *Rhizoctonia* alliance (Bonnardeaux et al. 2007). Because of the lack of data on the distribution of specific fungi it is not possible to use such data in ecological niche modelling.

As seed production in *Disa bracteata* is pollinator-independent there was no need to incorporate the potential distribution of any pollinator in order to get a more realistic potential distribution of this orchid. *Disa bracteata* appears to be self-pollinating as a result of the breakup of pollinia in the anther (Kurzweil and Johnson 1993). Generally, this is not beneficial for genetic variability, however it does enable it to produce a large number of seeds. High propagule pressure greatly enhances the chances of the establishment of invasive species (Colautti et al 2006). In fact, genetic variability seems to be less important as many successful invaders reproduce vegetatively. This is frequently the only mode of reproduction in some invasive species. This is often influenced by environmental conditions that are not suitable for the full development of a plant e.g. maturation of seeds. Ideally, even in such cases an invasive species may couple vegetative propagation with occasional sexual reproduction in order to respond to a suite of selective pressures and propagate efficiently (Atwater et al. 2017).

The environmental similarity between Australia and South Africa enabled some African plants to naturalize in Australia, such as *Chrysanthemoides monilifera* (Asteraceae) and *Asparagus asparagoides* (Asparagaceae), which are considered to be major environmental weeds in Australia and New Zealand (Thorp & Lynch 2000). While the visualization using PCA indicate a large overlap between the niches of African and invasive populations of *D. bracteata* they are not the same and that small difference is important as it influences the results of the niche identity test. Another interesting result is that the niche of invasive populations has changed over time as the colonization process has progressed. At the time of the first introduction, which was around 1945 (date of the first recorded specimen), only a few localities were known and the conditions there were similar to those in its natural range. However, over time more populations were established, which eventually gave rise to the colonization of the eastern part of Australia. First georeferenced specimen collected in 1989 was ~~collected~~ on the southern Adelaide Plains. Since then invasive populations tend to colonize a habitat not occupied by natural populations, which are either newly adapted or simply absent in Africa.

Another interesting result of this study is an indication of probable niche shift between natural and non-native populations of this orchid. The first invasive populations inhabited areas located mostly in eastern Australia that are climatically similar to its native range. Spread to the western part of the continent involved colonizing novel habitats or those that are not available to *Disa* in its native range (Supplementary file 3). This shift is congruent with the Köppen–Geiger climate classification system (Peel et al. 2007), which indicates that the difference in niches may be influenced by the climate availability or different preferences within both ranges. In Africa, six types of climates are occupied while in Australia two of them are completely absent and the majority of established populations occurs within Csb climate (Coastal Mediterranean). Additionally, there is a difference between Eastern and Western Australia: within the former second most frequent climate type is the Cfb (Marine With Mild Winter), while in the latter this position belongs to the Csa climate (Interior Mediterranean; Figure 5). Thus it is not an entirely new climate but rather a shift of the climatic preferences that may be attributed to the establishment of invasive populations in areas possessing different composition of available climates. However, it may be linked to novel preferences as well since all climates that are present in Africa are present in Australia. Interestingly, areas of some types of climate are less frequent in Africa and apparently are sparsely populated by *D. bracteata* but mainly by other *Disa s.l.* species. This may indicate that in its native distribution there are factors that prevent *D. bracteata* occupying this niche, such as biotic interactions (possibly with other closely related species) while in Australia this constraint is absent and *D. bracteata* is able to colonize this novel habitat. Studies on niche shifting species indicate this occurs in various areas (Broennimann et al. 2007, Elith et al. 2010) but it is relevant to fewer than 15% of plant invaders (Petitpierre et al. 2012). There are significant differences between the climatic niches occupied by invasive and native populations of another invasive species of orchid, *E. helleborine* (Kolanowska 2013), but in this case, no shift within the Köppen–Geiger climate was found. A study of the niche shifts of plants introduced into Australia found that none of 26 species included in this study changed their Köppen–Geiger climatic niche (Gallagher et al. 2010). In the case of *D. bracteata* there seems to be a significant difference in the proportion among climates in areas occupied in Africa and Australia (Fisher's Exact Test $p = 1.5\times 10^{-5}$). The same result is obtained when Africa is compared with Australia split into two groups (Africa vs. Eastern Australia: Fisher's Exact Test $p = 1.4\times 10^{-4}$, Africa vs. Western Australia: Fisher's Exact Test $p = 1.3 \times 10^{-3}$).

Thus *D. bracteata* may be the first record of such a shift within Australia. When estimating niche conservatism and changes in future range one needs to bear in mind that correct estimation of the latter is tricky because acquiring a new niche is an active process possibly linked to novel adaptations that may not be known at the time of a study (Thuiller et al. 2008, Elith et al. 2010).

Conclusions

A South African Orchid has become invasive in Australia and is already present on a large part of the continent. Models suggest that area with the suitable niche for this species is larger than that already occupied thus its spread will continue. How this spread will proceed depends on future changes in the factors influencing it and primarily on the magnitude of the change in climate. As demonstrated here it is very likely that a niche shift has occurred in this case so its further spread should be monitored. Altogether the results of this study indicate the necessity of further studies on the spread of *D. bracteata*, preferably including genetic differences between native and invasive populations.

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Figures

Fig. 1. The potential area of the suitable niche for *Disa bracteata* in Southern Africa. The insets visualize: A) Potential niche modelled using current climate and soil variables, B) Potential niche modelled using current climate variables, C) Potential niche modelled using rcp26 climate change scenario, D) Potential niche modelled using rcp45 climate change scenario, E) Potential niche modelled using rcp60 climate change scenario, F) Potential niche modelled using rcp85 climate change scenario. Blue indicates not suitable and red highly suitable. Green dots denote accessions used in ecological niche modeling. Lines show major rivers within the region. Maps were drawn using WGS 1984 (EPSG:4326) coordinate system.

Fig. 2. The potential area of the suitable niche for *Disa bracteata* in Australia and adjacent islands. The insets visualize: A) Potential niche modelled using current climate and soil variables, B) Potential niche modelled using current climate variables, C) Potential niche modelled using rcp26 climate change scenario, D) Potential niche modelled using rcp45 climate change scenario, E) Potential niche modelled using rcp60 climate change scenario, F) Potential niche modelled using rcp85 climate change scenario. Blue indicates not suitable and red highly suitable. Purple

dots denote accessions used in ecological niche modeling. Lines show administrative borders. Maps were drawn using WGS 1984 (EPSG:4326) coordinate system.

Fig. 3. Environmental niche of *Disa bracteata* as visualized by principal component analysis (PCA). Diagram was constructed with environmental values recorded for natural and invasive populations. Blue background indicates the whole environment included in the analysis present in Africa and Australia. Native and invasive populations are enclosed by circles encompassing 95% of the data. While native populations occupy a slightly broader niche some of the invasive populations occupy habitats not present in its native niche.

Fig. 4. Boxplot diagram of the environmental values recorded in the areas of occurrence of natural and invasive populations of *Disa bracteata*. In addition to examining invasive populations as a whole they are divided into Western Australia (W-AUS) and Eastern Australia (E-AUS). Bio15 – Precipitation Seasonality (CoV), bio18 – Precipitation in the Warmest Quarter [mm], bio19 – Precipitation in the Coldest Quarter [mm], bio7 – Temperature Annual Range [°C], bio8 – Mean Temperature in the Wettest Quarter [°C], soil.organic.carbon content is expressed in [g per kg], Soil.pH refers to a pH x 10 in H_2O, Sand.content is expressed as a mass fraction in percent. Areas are compared to each other using T-tests. Circles are means, horizontal lines minimum and maximum values, the box represents first and third quantiles, and vertical line inside delineates the median.

Fig. 5 Histogram of climates recorded in the known populations divided into: natural (South African), invasive (Australian), E-AUS (Eastern Australian), and W-AUS (Western Australian). Two types of climate present in Africa are not occupied in Australia. Invasive populations occur mainly within Csb climate with Cfb as the second most frequent in the Eastern Part and Csa as the second one in the Western Part of Australia. Shortcuts follow standard Köppen–Geiger climate classification system: BSh - Hot Semi-Arid, BSk - Cold Semi-Arid, Cfa - Humid Subtropical, Cfb - Marine - Mild Winter, Csa - Interior Mediterranean, Csb - Coastal Mediterranean. Prior to the analysis occurrences were rarified to match resolution of climate map (10 km^2).

Supplementary file 1. List of localities used in the ecological niche modeling.

Supplementary file 2. Initial variables used by MaxentVariableSelection to choose appropriate set of variables and betamultiplier. Topographic variables marked with “Calculated*” as a source were calculated with “raster” package in R using function “terrain” on altitude dataset. Variables used for modeling are marked with bold. All variables were used for PCA.

Supplementary file 3. PCA diagram displaying environmental values recorded for the populations studied. Points are coloured according to the decade in which they were recorded. Groups for a particular decade have different colour assignments and are enclosed in a circle encompassing 95% of the data. There is a visible shift in invasive populations, which move towards negative axis values.

Table 1(on next page)

Results of bias metric.

If invasive populations would occupy the same habitat as natural the result will be 0. Negative values indicate occupation of sites below median found in the natural range, whereas positive values indicate occupation of sites above the median. The greater the number is (or lower in case of negative values) the greater is the difference.

	bio07	bio08	bio15	bio18	bio19	Sand content	Soil Organic Carbon Content	Soil pH
Australia	24.9	-23.6	-6.0	-10.5	-7.1	47.6	14.7	-14.3
Eastern Australia	27.9	-24.9	-8.8	-10.3	-8.0	47.6	16.0	-14.3
Western Australia	6.2	-4.0	11.9	-12.9	10.5	52.4	-2.0	-4.8

Table 1 – Results of bias metric. If invasive populations would occupy the same habitat as natural the result will be 0. Negative values indicate occupation of sites below median found in the natural range, whereas positive values indicate occupation of sites above the median. The greater the number is (or lower in case of negative values) the greater is the difference.

Figure 1

The potential area of the suitable niche for *Disa bracteata* in Southern Africa.

The insets visualize: (A) Potential niche modelled using current climate and soil variables, (B) Potential niche modelled using current climate variables, (C) Potential niche modelled using rcp26 climate change scenario, (D) Potential niche modelled using rcp45 climate change scenario, (E) Potential niche modelled using rcp60 climate change scenario, (F) Potential niche modelled using rcp85 climate change scenario. Blue indicates not suitable and red highly suitable. Green dots denote accessions used in ecological niche modeling. Lines show major rivers within the region. Maps were drawn using WGS 1984 (EPSG:4326) coordinate system.

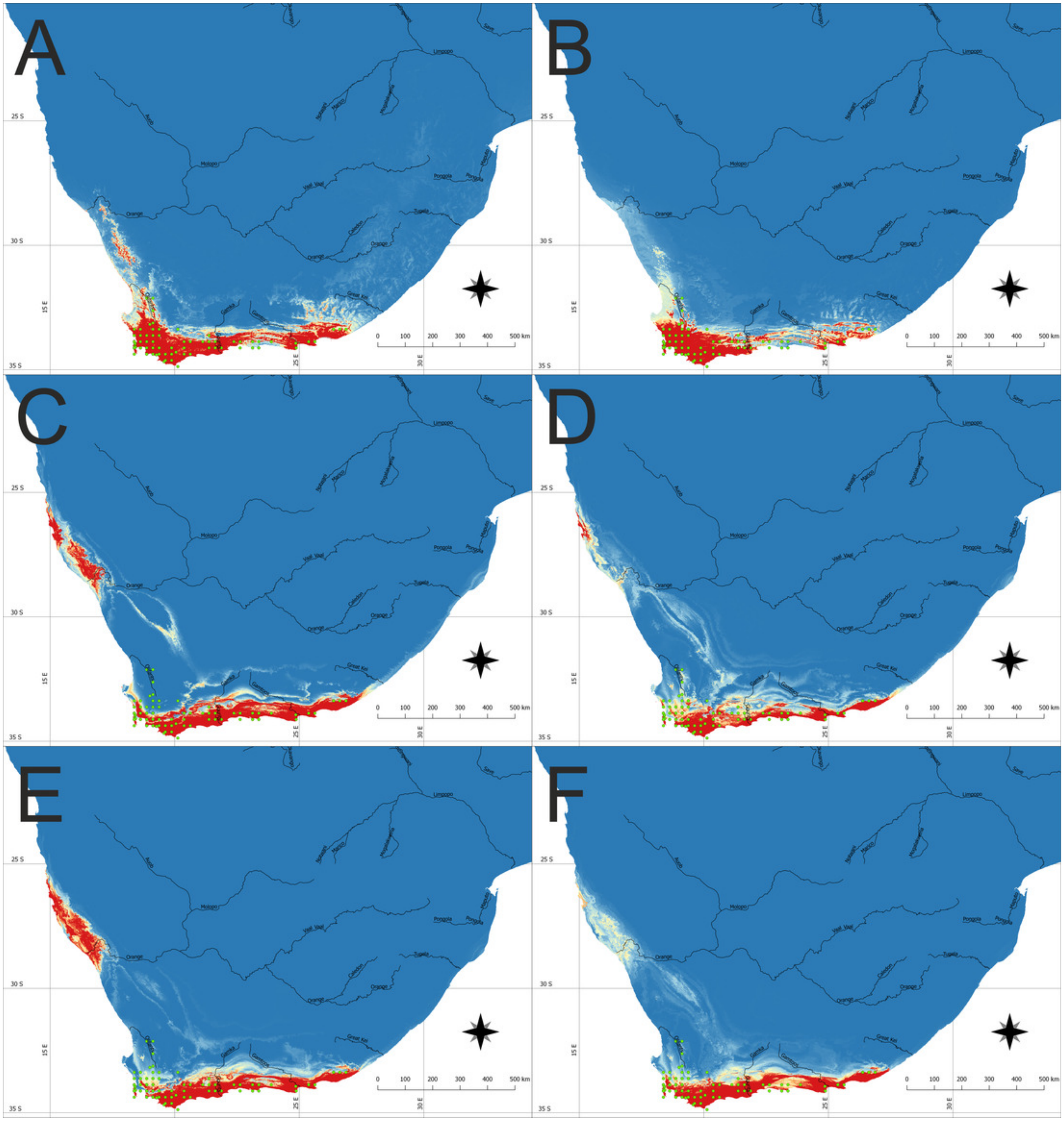

A
B
C
D
E
F
25 S
30 S
35 S
15 E
25 E
30 E
0 100 200 300 400 500 km

Figure 2

The potential area of the suitable niche for *Disa bracteata* in Australia and adjacent islands.

The insets visualize: (A) Potential niche modelled using current climate and soil variables, (B) Potential niche modelled using current climate variables, (C) Potential niche modelled using rcp26 climate change scenario, (D) Potential niche modelled using rcp45 climate change scenario, (E) Potential niche modelled using rcp60 climate change scenario, (F) Potential niche modelled using rcp85 climate change scenario. Blue indicates not suitable and red highly suitable. Purple dots denote accessions used in ecological niche modeling. Lines show administrative borders. Maps were drawn using WGS 1984 (EPSG:4326) coordinate system.

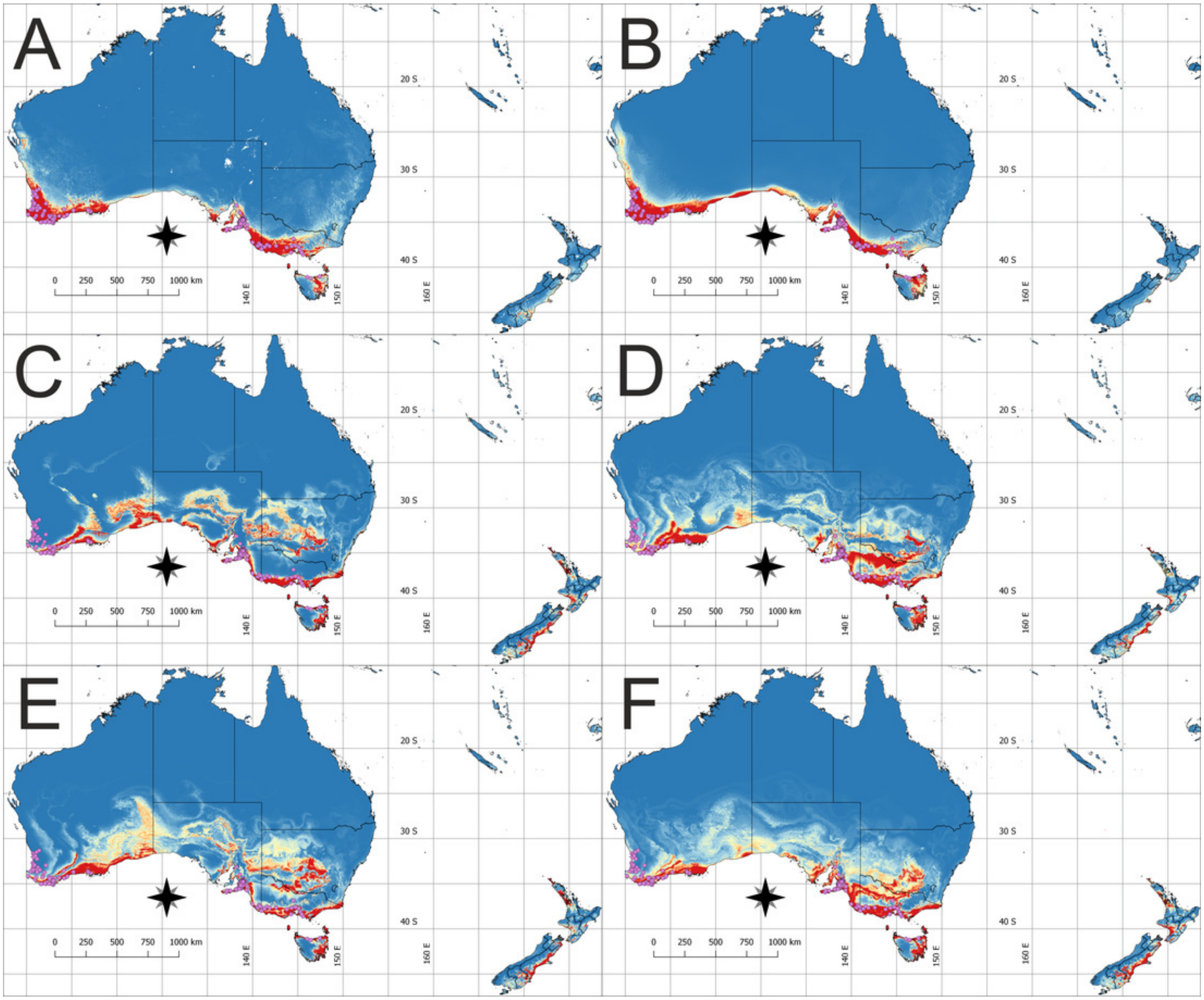

A
B
C
D
E
F
20 S
30 S
40 S
0 250 500 750 1000 km
140 E
150 E
160 E

Figure 3

Environmental niche of *Disa bracteata* as visualized by principal component analysis (PCA).

Diagram was constructed with environmental values recorded for natural and invasive populations. Blue background indicates the whole environment included in the analysis present in Africa and Australia. Native and invasive populations are enclosed by circles encompassing 95% of the data. While native populations occupy a slightly broader niche some of the invasive populations occupy habitats not present in its native niche.

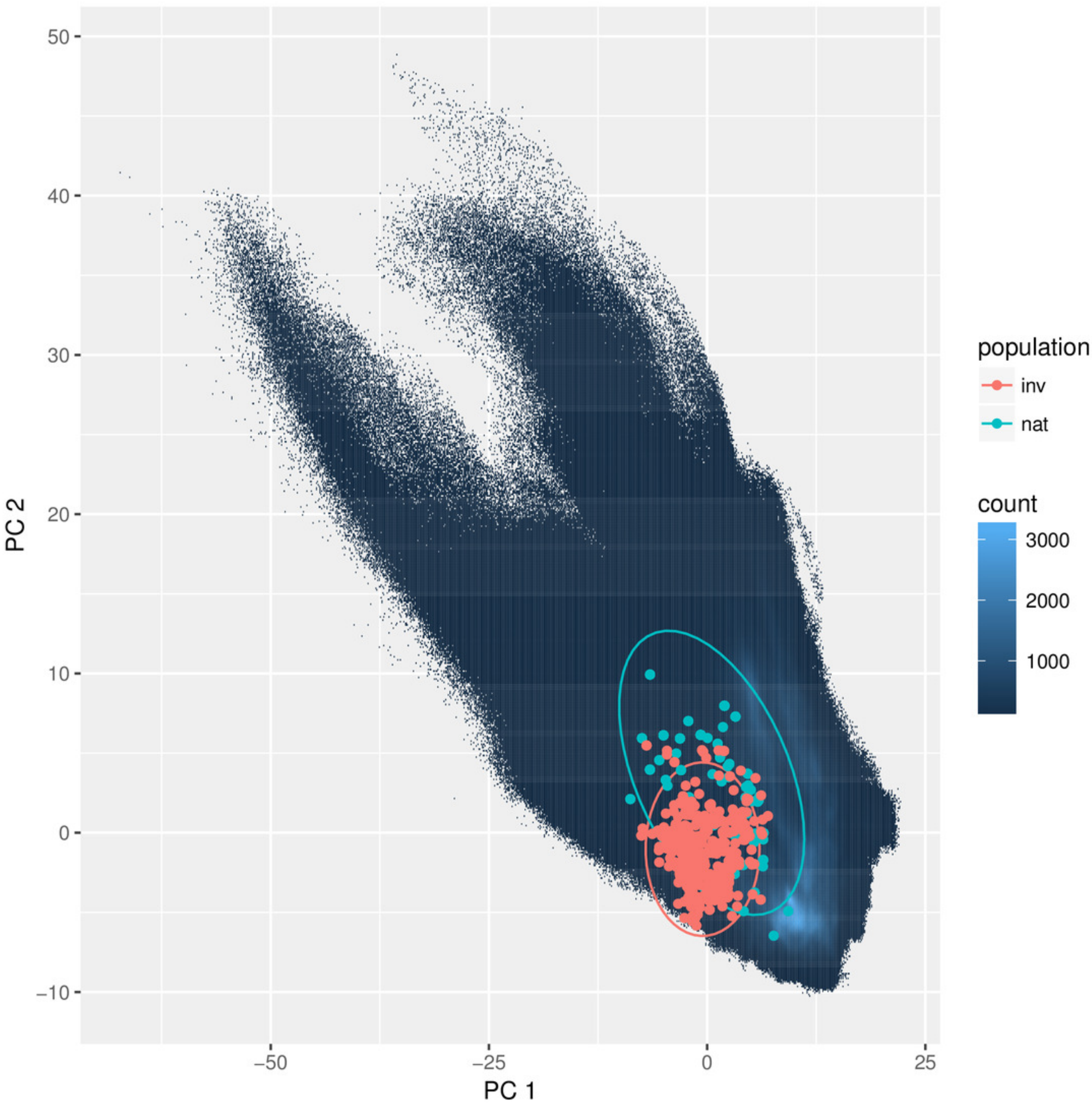

50
40
30
20
10
0
−10
PC 2
−50
−25
0
25
PC 1
population
inv
nat
count
3000
2000
1000

Figure 4

Boxplot diagram of the environmental values recorded in the areas of occurrence of natural and invasive populations of *Disa bracteata*.

In addition to examining invasive populations as a whole they are divided into Western Australia (W-AUS) and Eastern Australia (E-AUS). Bio15 – Precipitation Seasonality (CoV), bio18 – Precipitation in the Warmest Quarter [mm], bio19 – Precipitation in the Coldest Quarter [mm], bio7 – Temperature Annual Range [°C], bio8 – Mean Temperature in the Wettest Quarter [°C], soil.organic.carbon content is expressed in [g per kg], Soil.pH refers to a pH x 10 in H_2O, Sand.content is expressed as a mass fraction in percent. Areas are compared to each other using T-tests. Circles are means, horizontal lines minimum and maximum values, the box represents first and third quantiles, and vertical line inside delineates the median.

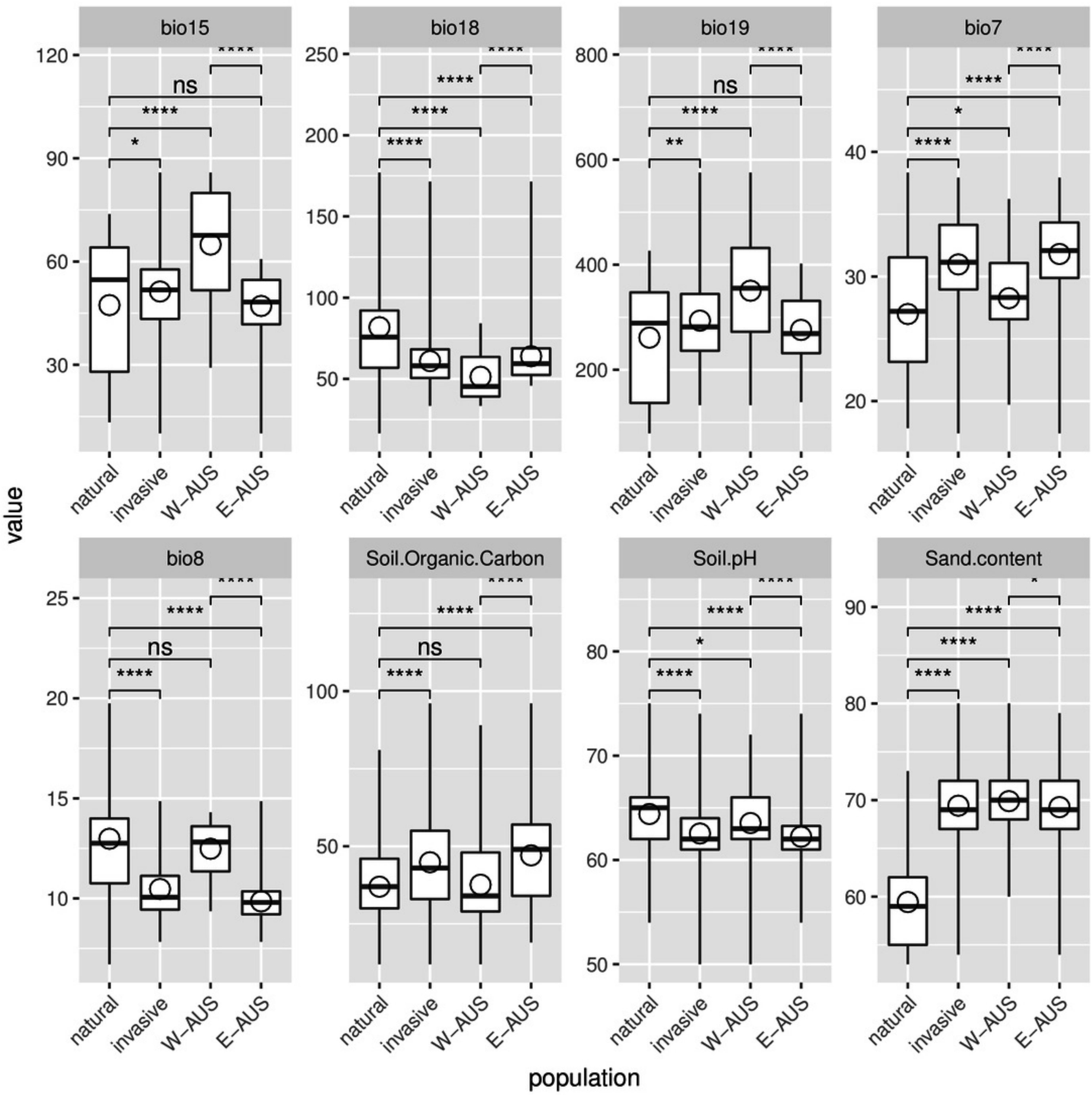
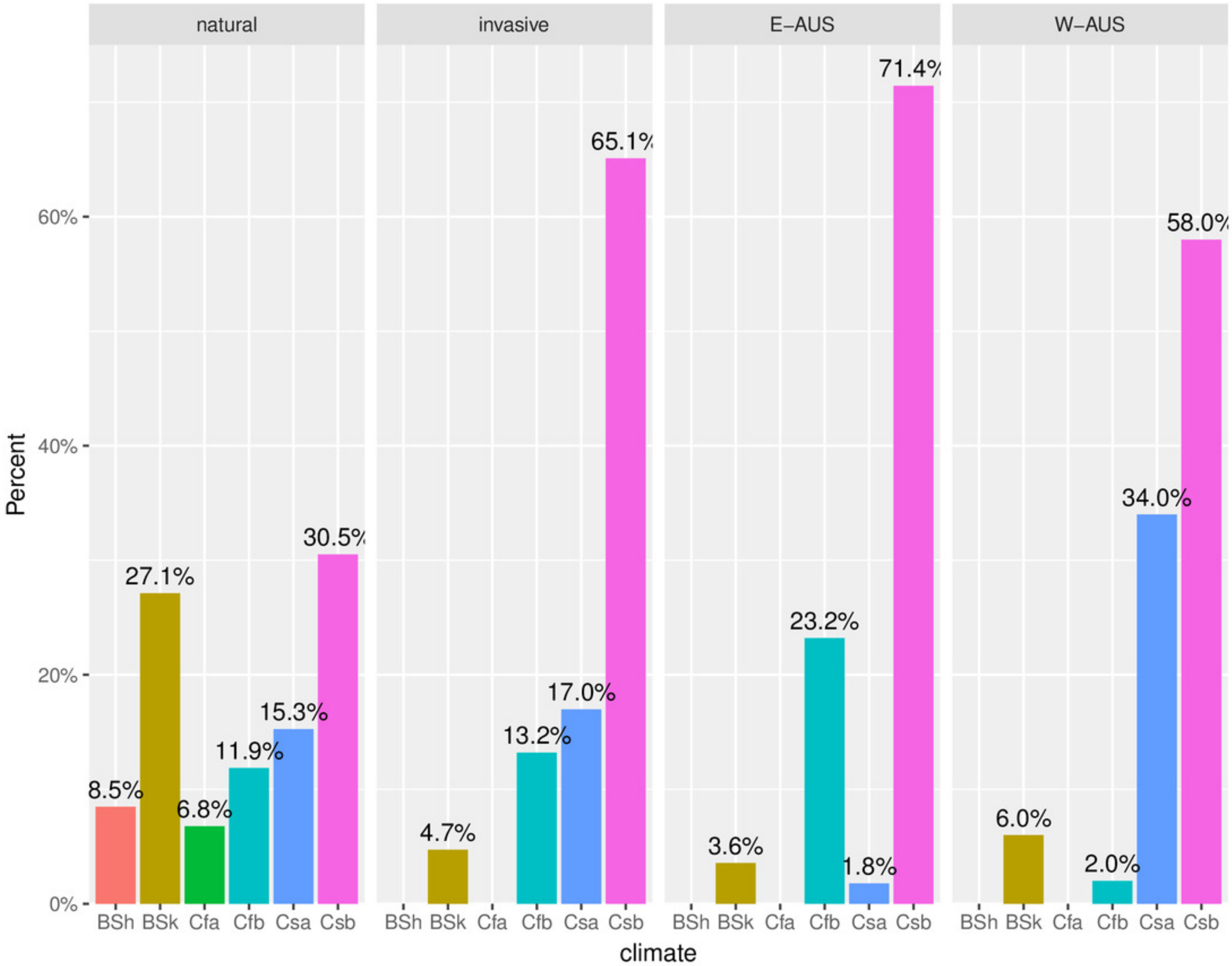

bio15
bio18
bio19
bio7
bio8
Soil.Organic.Carbon
Soil.pH
Sand.content
value
population
natural
invasive
W–AUS
E–AUS
ns
****
**
*

Figure 5

Histogram of climates recorded in the known populations divided into: natural (South African), invasive (Australian), E-AUS (Eastern Australian), and W-AUS (Western Australian).

Two types of climate present in Africa are not occupied in Australia. Invasive populations occur mainly within Csb climate with Cfb as the second most frequent in the Eastern Part and Csa as the second one in the Western Part of Australia. Shortcuts follow standard Köppen–Geiger climate classification system: BSh - Hot Semi-Arid, BSk - Cold Semi-Arid, Cfa - Humid Subtropical, Cfb - Marine with Mild Winter, Csa - Interior Mediterranean, Csb - Coastal Mediterranean. Prior to the analysis occurrences were rarified to match resolution of climate map (10 km^2).


natural
invasive
E-AUS
W-AUS
Percent
60%
40%
20%
0%
8.5%
27.1%
6.8%
11.9%
15.3%
30.5%
4.7%
13.2%
17.0%
65.1%
3.6%
23.2%
1.8%
71.4%
6.0%
2.0%
34.0%
58.0%
BSh BSk Cfa Cfb Csa Csb
climate