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Understanding environmental factors influencing invasion of *Lilium formosanum* in Mpumalanga Province and models of its potential distribution in South Africa

by

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DECLARATION:

I, Mosiuoa Walter Bereng declare that the dissertation, which I hereby submit for the degree Master of Science (Environmental Ecology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date: 8 July 2014

ABSTRACT

Alien invasive plants are of concern in the world because of their potential to spread into the natural environment. Invasion patterns observed in plant species can be attributed among other things to favourable environmental conditions. Understanding invasion dynamics of alien invasive plants can help in timely intervention initiatives. In Mpumalanga, *Lilium formosanum* (Liliaceae) appears to be an emerging plant invader and is spreading in the natural environment. The study investigated the invasion extent and predictor variables which could explain abundance patterns of *L. formosanum* in the invasive range in Mpumalanga province in South Africa and further predict regions of the world that could be climatically suitable. *Lilium formosanum* was surveyed along 11 major routes leading into the towns of Sabie and Graskop in Mpumalanga from a slow moving vehicle. A total of 241 kilometres was surveyed. *Lilium formosanum* was found to be invasive from the towns of Sabie and Graskop. Climatically suitable areas were predicted using DIVA-GIS and climate data was obtained from WORLDCLIM database while occurrence records were obtained from the Southern African Plant Invaders Atlas, Australia's virtual herbarium and the Global Biodiversity Information Facility. In conclusion, distance, altitude and route were found to have an influence on the abundance of *L. formosanum* in Mpumalanga Province. Climatically suitable areas included the eastern coastal belt, northern provinces and the interior parts of South Africa including major parts of Limpopo and Mpumalanga.

Key words: *Lilium formosanum*, Alien invasive species, DIVA-GIS, Climatically suitable, abundance pattern, Mpumalanga.

INTRODUCTION

Many plant species have considerably expanded their distribution due to human activities. Humans have moved native species intentionally and accidentally across their natural dispersal barriers (Kolar & Lodge, 2001; Blackburn *et al*. 2011; Rejmànek *et al*. 2005) and the movement around the world has been due to trading activities (Dogra *et al.* 2010). According to Blackburn *et al*. (2011), all these introduced species have the potential to become invaders by crossing a series of barriers. Having crossed the geographic barrier, species still have to overcome environmental barriers (Blackburn *et al*. 2011) in order to grow, reproduce and spread further. Many species were initially moved beyond their dispersal limit with the intention of managed cultivation, however, they eventually became established in the natural environment. Having escaped into the natural environment does not necessarily mean that the species will be invasive, it still has to adapt to the new environment.

While in their native range, species populations are usually constrained by a range of abiotic and biotic factors and when moved to a different environment, they encounter a different set of factors which influence their abundance (Hierro *et al.* 2005). For example, *Cytisus scoparius* (Fabaceae) is native in Europe, but it appears to perform better in its introduced areas than in the native range (Buckley *et al.* 2003). Better performance in introduced habitat was attributed to increased seed size due to a different set of environmental factors compared to its native range. Also *Solidago gigantea* (Asteraceae) grows more vigorously in its invasive range in Europe than in its native range of North America due to low winter and high summer temperatures (Jakobs *et al.* 2004).

Invasion of species in a specific habitat has been attributed to many factors including, but not limited to, propagule pressure (Richardson 2004; Hierro *et al*. 2005), habitat compatibility and the propagule pressure (Rejmànek *et al*. 2005) for it to be invasive. Enough propagules are needed for a species to maintain a population and to spread to new areas. But if the receiving environment is not conducive for the species, i.e. resistant to the introduced species, the rate of propagule supply needs to be high to overcome the constraints of the receiving environment (Richardson 2004; Richardson and Pyšek 2006).

Lilium formosanum (Liliaceae) has been moved beyond its dispersal barriers by humans and it reached areas like South Africa, where it was cultivated for ornamental purposes (ARC-PPRI 2007). However, the plant managed to overcome the captivity barrier, and is now in the natural environment. From literature, there are no exact records on the year of introduction in South Africa, therefore when estimating its occurrence in South Africa we can use the minimum residence time based on herbarium specimens (Rejmànek *et al*. 2005) which is used to estimate the introduction of a taxon. The available *L. formosanum* specimen is at South African National Biodiversity Institute, National Herbarium which dates the collection as 1980, indicating it as a naturalised garden escape collected on a road between Sabie and Lydenburg. However, it should be noted that this is not the year of introduction, but rather when a specimen was collected from the wild. It is now a naturalized invasive plant in the midlands of KwaZulu-Natal and it is considered to invade anthropogenically disturbed habitats such as roadside verges, plantation edges and natural grasslands (Rodger *et al.* 2010).

In South Africa, *L. formosanum* is an emerging invasive plant with signs of spread in provinces of South Africa such as KwaZulu-Natal, Limpopo and Mpumalanga. It is listed as a category 3 invasive plant species in terms of Conservation of Agricultural Resources Act No. 43 of 1983 (CARA). Category 3 species have shown potential of being invasive and further growing, propagation or trade of the plant is prohibited.

In order to best direct resources for management of invasive plant species like *L. formosanum* in their invasive range, it is necessary to understand its invasion dynamics. Understanding its invasion dynamics will involve understanding of the invasion front of *L. formosanum* from the source towns of Sabie and Graskop as well as environmental limiting factors to better control further spread.

Distribution of plant species, both native and invasive species, is influenced by climatic conditions. Correlative statistical approaches can be used to predict climatically suitable areas of a plant present in one location to a climatically suitable environment elsewhere. These approaches, termed Species Distribution Models, are used to predict the current and future distribution of species based on their climatic requirements (Beaumont *et al.* 2005; Guisan & Thuiller 2005; Elith & Leathwick 2009). *Lilium formosanum* is a plant endemic to subtropical islands in the Ryukyu Archipelago and Taiwan but occurs in South Africa and Australia in the natural environment and areas vulnerable to future invasions by the species can be predicted.

However, the management strategy of *L. formosanum* should not only focus on the already invaded areas but to areas which are likely to be invaded for pro-active management. In order to develop a pro-active strategy, there should be a form of early warning system for climatically suitable areas which might be invaded. As a result this study will focus on understanding factors contributing to *L. formosanum* invasiveness and predicting climatically suitable areas elsewhere.

Aims of the study were to: a) determine the extent and patterns of abundance of *L. formosanum* invasion in the Sabie-Graskop region of Mpumalanga; b) identify factors that could explain the abundance of the plant in the study area; and c) identify regions of the world that are likely to be climatically suitable for *L. formosanum* invasion.

In this study, we hypothesized that distance from the two towns of Sabie and Graskop has a significant effect in the *L. formosanum* abundance and its invasion.

MATERIALS AND METHODS

Study species

Lilium formosanum is a bulbous plant with a height reaching 1.5–2 m high. The plant is endemic to subtropical islands in the Ryukyu Archipelago and Taiwan (Hiramatsu *et al.* 2002a). In its native range, the plant occurs at an altitude ranging from sea level to an altitude of 3000 m a.s.l. (Hiramatsu *et al.* 2001; Wen & Hsiao, 2001). Its abundance pattern differs greatly with altitude, ranging from lower abundance at lower altitude and increasing abundance with increasing altitude (Hiramatsu *et al*. 2001). *Lilium formosanum* is a self-compatible plant and in some populations out-crossing dominates, while selfing dominates within others (Hiramatsu *et al.* 2001). Selfing is considered to play a major role in establishing new populations from a single introduction (Hiramatsu *et al.* 2001). In its native range, it is found in areas which are frequently disturbed naturally, like in areas prone to landslides (Hiramatsu *et al.* 2002b; Warner *et al*. 2006). In South Africa, it is mostly found in disturbed land areas like along road edges and the edges of tree plantations (ARC-PPRI 2007) where there is frequent disturbance.

Study area

The study was conducted in Mpumalanga province in South Africa, a warm summer-rainfall province that contains three of South Africa's nine biomes including grassland, savanna and forest (Ferrar & Lötter 2007). The study area was centred on the towns of Sabie (25˚46'S; 30˚46'E) at 1092 m a.s.l and Graskop (24˚55'S; 30˚48'E) at 1487 m a.s.l which are thought to be the sources of *L. formosanum*. The study area lies on the Highveld of Mpumalanga with the rainfall above 500 mm/yr (Ferrar & Lötter 2007). Two areas of concern were along the roadside verge and the plantation edges, areas which are highly anthropogenically disturbed and commonly invaded by *L. formosanum*.

Sampling method

The abundance of *L. formosanum* was recorded along 11 major roads leading into Sabie and Graskop (Table 1). Observations were made from a slow moving vehicle along the road verge and abundance estimates were made per kilometre section of road. The study was conducted in February (2012) when the plant flowers. A total distance of 241 km was surveyed. The survey protocol consisted of two trips, one away from the towns to check for presence of the plant and the other was towards the towns to assess the abundance. The abundance survey started approximately 5 km beyond the last recorded presence of the plant. The abundance of the plant within each kilometre strip was recorded using a five-category abundance scale, as it was impractical to count all of the individuals given the amount of time that this would take (Table 2).

Table 1. Route number and description of all roads leading into Sabie and Graskop which were surveyed in the study, together with the distance (km) travelled on each route.

Route Number	Route description	Distance surveyed
1	Hazyview to Sabie R 536	30
2	Whiteriver to Sabie R 537	36
3	Blyde canyon to Graskop R 532	28
4	Sabie to Graskop R 37	11
5	Graskop to Sabie R 37	10
6	Pilgrim’s rest to Graskop R 36	9
7	Hazyview to Graskop R 535	23
8	Bushbuckridge to Graskop R 533	22
9	Lydenburg to Sabie R 37	31
10	Sudwala to Sabie R 534	3
11	Brondal to Sabie R 40	38

Table 2: The abundance ratings which were used to record the plant abundance within each kilometre strip.

Rating	Description
0	No individuals
1	Population ≤25 individuals
2	Sparse cover with populations 26-50 individuals
3	≥ 50 More or less continuous cover but with gaps
4	Continuous cover and or abundant populations

Data analysis

All analyses were conducted using SAS with a total of 251 observations from the study area. Six predictor variables were used to determine which variables best explain the abundance of the *L. formosanum.* These included: minimum temperature of the coldest month (Bio6), maximum temperature of the warmest month (Bio5), annual precipitation (Bio12), annual mean temperature (Bio1), distance to the nearest town and altitude. Climatic variables were downloaded from world climatic data (http://www.worldclim.org). Distance to the nearest town was calculated as distance in kilometres travelled from the last plant recorded away from town to the plant recorded closest to town. For distance between Graskop and Sabie, since the two towns have one route connecting each other, the distance was split at half way from each town and observations were done starting from the split point into each town.

Predictor variables explaining *L. formosanum* abundance

Logistic regression was considered to be the best approach for determining which predictor variables best explained the abundance of *L. formosanum* because it is best suited for studying categorical data (Peng *et al.* 2002). The first model that was developed was a multiple logistic regression model with presence/absence as the response variable and all environmental predictors as the explanatory variables. However, the multivariate model gave very high standard errors which indicated that the results were highly unstable and as a result was considered to be unreliable. This could be due to few observations in relation to the number of explanatory variables used in the multivariate model. It was thus decided to produce a series of univariate logistic models with presence/absence as the response variable and 251 observations were used in the analysis. Then more models were produced with distance as a co-variable and route number, altitude class (Appendix 1) and annual precipitation class (Appendix 2) as explanatory variables. In these models, data for route number 4 and 6 were excluded due to extremely high standard errors and resulted with 230 observation used in the analysis.

To determine which route was more favourable for the abundance of *L. formosanum*, I considered the odds ratio from the logistic regression model. Where the odds ratio value was greater than 1, it indicated that as the predictor increases, the odds of the outcome occurring increases as well. In the event that the value was less than 1, I looked at the reciprocal of the value (i.e. I divided 1 by the estimate value). To determine which altitude class and annual precipitation class best explained abundance of *L. formosanum*, I used the odds ratio. Altitude and precipitation values were lumped into classes for practical analysis of the results. Predictor variables used in the models were first checked for their correlation with one other using Pearson correlations, and where there was high correlation, with correlation coefficient greater than 0.8 or larger than -0.8, only one variable was used.

Occurrence records for distribution models

The native records of *L. formosanum* (from Ryukyu Archipelago and Taiwan) were sourced from the Global Biodiversity Information Facility (GBIF) online database (http://gbif.org) with only 65 records being obtained.

In its invasive range in KwaZulu-Natal; 189 records were obtained from the South African Plant Invaders Atlas (SAPIA) (Henderson, 2007), 362 records were obtained from surveys (Michael Braack pers. comm.). A total of 257 records were obtained from field surveys in Mpumalanga province.

In Australia, the plant was been reported as being invasive on Lord Howe Island world heritage site (Warner *et al.* 2006). These records were sourced from Australia's virtual herbarium (http://avh.ala.org.au) online database. A total of 65 records were available where the species was known to be invading the natural environment (cultivated specimens were ignored).

Predictor variables

Environmental data for predicting the potential distribution of *L. formosanum* was obtained from WORLDCLIM (http://www.worldclim.org/) downloaded at a spatial resolution of 10 minutes (Hijmans *et al*. 2005). From the WORLDCLIM, 19 climate variables were obtained (Appendix 3). Two sets of predictor variables were used in the models. The model used all 19 climatic variables and the second model used only four climatic variables which I believed to have most relevant for the distribution of *L. formosanum* and they were: annual mean temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6) and annual precipitation (Bio12).

Predicting climatically suitable areas

Models of the potential distribution of *L. formosanum* were produced using the Bioclim algorithm in DIVA-GIS version 7.5 (Hijmans *et al*. 2012) using records obtained from the native range (Taiwan) and invasive range (South Africa and Australia). Four different models were developed, each one with a different combination of occurrence records and predictor variables. The first model was calibrated with a set of all known occurrence records and four predictor variables, while the second model was calibrated with South African records and four predictor variables. The third model was calibrated using all known occurrence records and 19 predictor variables and the fourth model was calibrated with South Africa records and 19 predictor variables for predicting climatically suitable areas in Southern Africa region. In the Asian region and Australia, the model was calibrated using native records, four predictor variables and 19 predictor variables respectively. The fifth model was calibrated with native and Australian records using four predictor variables and 19 predictor variables. In the Bioclim algorithm, the True/False output was used at a threshold of zero. The True/False output is equivalent to maximums and minimums.

RESULTS

Invasion extent and abundance patterns

Lilium formosanum was recorded along all major routes leading into Graskop and Sabie (Fig. 1). *Lilium formosanum* was recorded immediately as one left town on some routes. The closest record of *L.formosanum* to town was at about 0.12 km on route 9, 0.49 km on route 2 and at 0.58 km at route 4 from the nearest town. On routes 1, 5, 3 and 7, the first plant recorded was comparatively far from the town and a distance of 0.9 km, 0.8 km, 1.94 km and 1.40 km respectively.

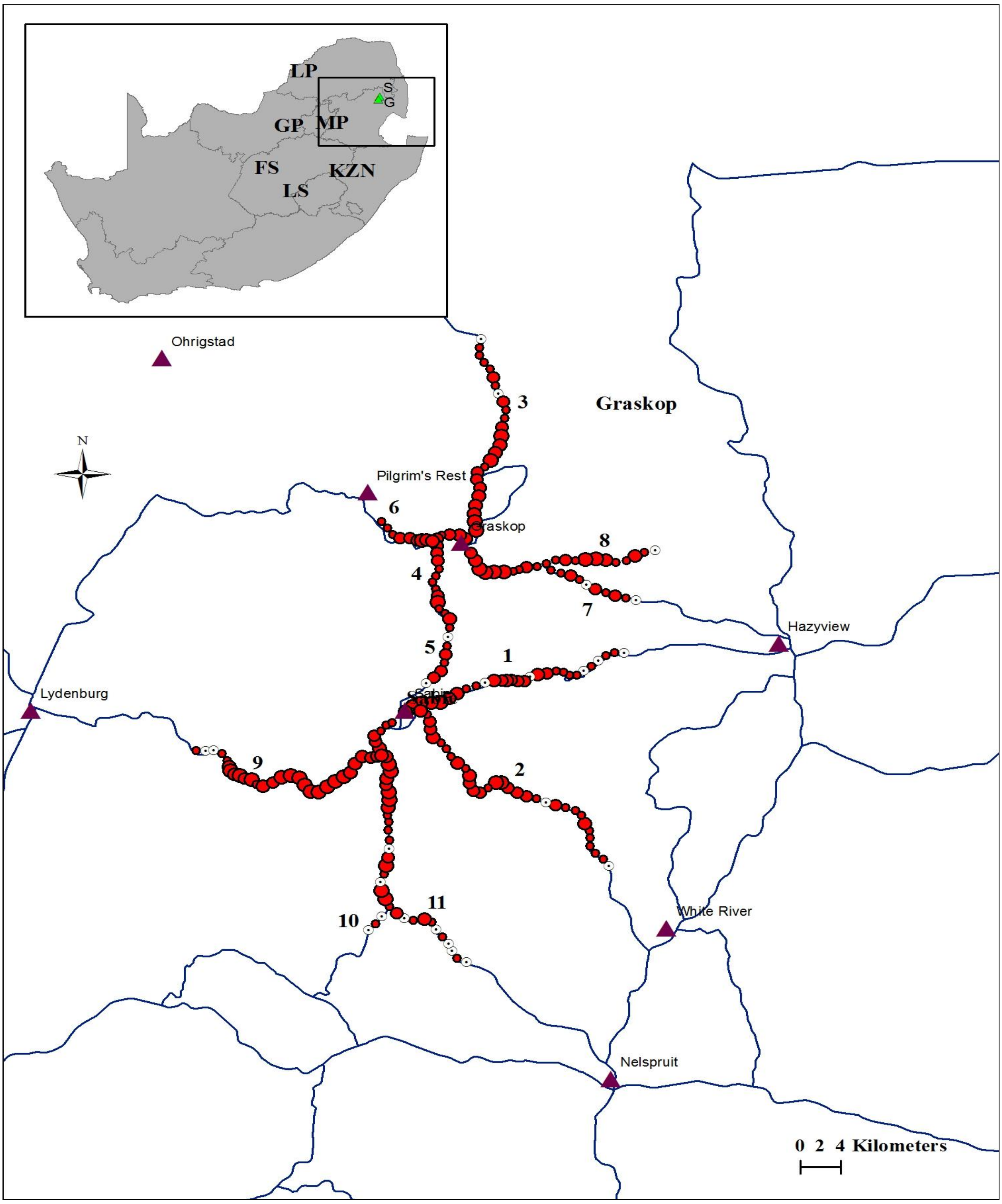

Figure 1. Abundance of the *Lilium formosanum* in 1 kilometre sections along major roads from the towns of Sabie and Graskop in Mpumalanga which are believed to be the source of *Lilium formosanum* invasion in South Africa. Large red dots indicate high abundance with continuous cover while small red dots indicate lower abundance. White dots indicate absence. The numbers on the map refer to route numbers and route name with their description outlined in Table 1.

Predictor variables explaining *L. formosanum* abundance

Three of the six models explain a significant amount of variation ($p < 0.05$) on *L. formosanum* abundance, including distance ($p \leq 0.001$), altitude ($p \leq 0.001$) and distance and route number ($p = 0.005$) (Table 3). Annual precipitation did not have a significant effect, but the (p-value of 0.05) indicated that it was marginally significant. Abundance of *L. formosanum* clearly declined with distance from the two towns (Fig. 2). The abundance of *L. formosanum* appeared to be relatively high up to a distance of 25–30 km away from town after which abundance declined at a distance of 35–40 km, where the lowest abundance was recorded at 40–45 km. The abundance of *L. formosanum* increased with increasing altitude up to 1600–1900 m a.s.l where it reached maximum abundance (Fig. 3). However, its abundance was much lower at high altitude 2000–2100 m a.s.l (Fig. 3). There appears to be collinearity between distance and altitude as the average altitude of the distance classes that were furthest away (35-40 km and 40-45 km) from the two towns are lowest (Fig. 4).

Further checks of how *L. formosanum* abundances varied with reference to altitude were conducted using the odds ratio (Table 4), whereby the estimate value was used to interpret relationship between altitude and abundance. From the altitude classes used in the analysis, altitude range (1500–1900 m a.s.l) in Table 4 had a 8.33 fold greater chance having plant preference compared to altitude range (700–1100 m a.s.l) and (1100–1500 m a.s.l) suggesting that the species prefers higher altitudes compared to lower altitudes. *Lilium formosanum* abundance does not appear to be strongly affected by annual precipitation, but it was not recorded at areas with low precipitation (Fig. 5). High abundance was recorded at localities with higher precipitation class as indicated by the precipitation class above 1100 mm. In its native range, the plant seems to occur in higher precipitation areas (Fig. 6a) while in the invasive ranges of South Africa and Australia, the plant seems to occur in comparatively lower rainfall areas.

Table 3. Summary of results of logistic regression models with six models used. Significant ($p < 0.05$) explanatory variables are indicated by *.

Model	Explanatory variables	P-value
1	Distance *	<0.001
2	Altitude *	<0.001
3	Annual precipitation	0.05
4	Distance + Route number *	0.005
5	Distance + Altitude class	0.198
6	Distance + Annual precipitation class	0.067

Table 4. Results from models using presence as the response and explanatory variables: distance and route number in model 1, distance and altitude class in model 5 and distance and annual precipitation in model 6). Only significant ratios are shown.

Model	Contrast	Estimate	Standard Errors	Confidence Limits		Wald	P-value
Dist Route	R1/R2	0.06	0.05	0.01	0.33	10.66	0.001
	R1/R7	0.13	0.10	0.03	0.62	6.68	0.010
	R1/R9	0.03	0.03	0.01	0.20	13.69	0.000
	R1/R11	0.07	0.06	0.02	0.34	11.15	0.001
	R2/R3	13.79	11.99	2.51	75.82	9.11	0.003
	R2/R5	69.73	84.16	6.55	742.70	12.37	0.000
	R2/R8	8.15	8.67	1.01	65.55	3.89	0.049
	R3/R7	0.15	0.12	0.03	0.73	5.50	0.019
	R3/R9	0.04	0.04	0.01	0.24	12.10	0.001
	R3/R11	0.08	0.07	0.02	0.41	9.36	0.002
	R5/R7	0.03	0.03	0.00	0.27	9.84	0.002
	R5/R9	0.01	0.01	0.00	0.08	15.77	<.0001
	R5/R11	0.02	0.02	0.00	0.17	11.94	0.001
	R8/R9	0.06	0.07	0.01	0.56	6.11	0.014
	R9/R10	23.43	33.69	1.40	392.40	4.81	0.028
Dist Altclass	OAC1/OAC3	0.12	0.12	0.01	0.91	4.19	0.041
	OAC2/OAC3	0.12	0.12	0.01	0.93	4.13	0.042
Dist APclass	NAP1/NAP2	0.28	0.17	0.08	0.93	4.35	0.037
	NAP2/NAP4	4.91	3.30	1.32	18.34	5.61	0.018
	NAP4/NAP5	0.19	0.16	0.04	0.96	4.02	0.045

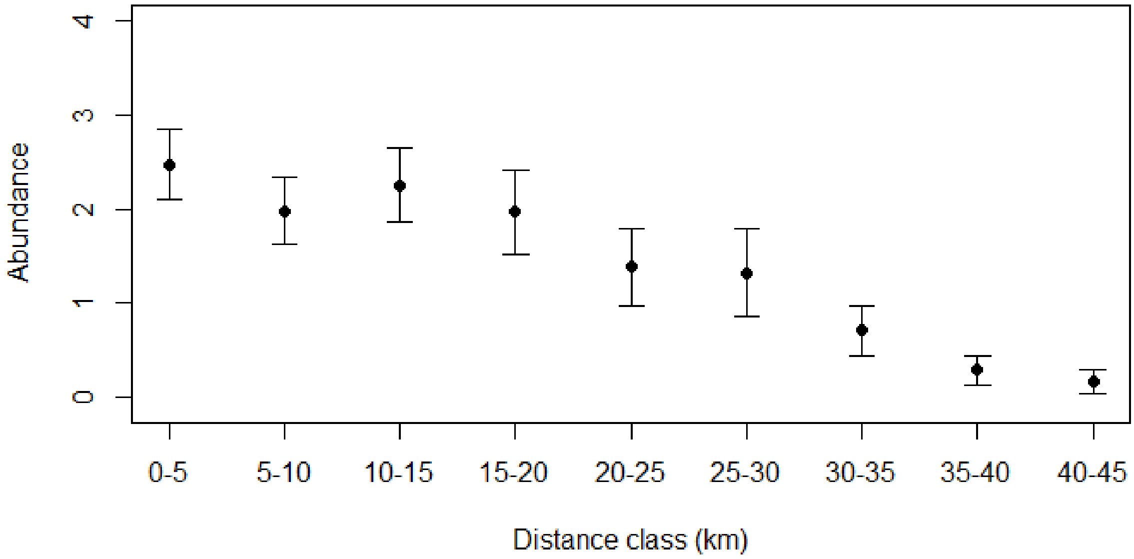

Figure 2. Species abundance (mean and standard error) across distance in the study area.

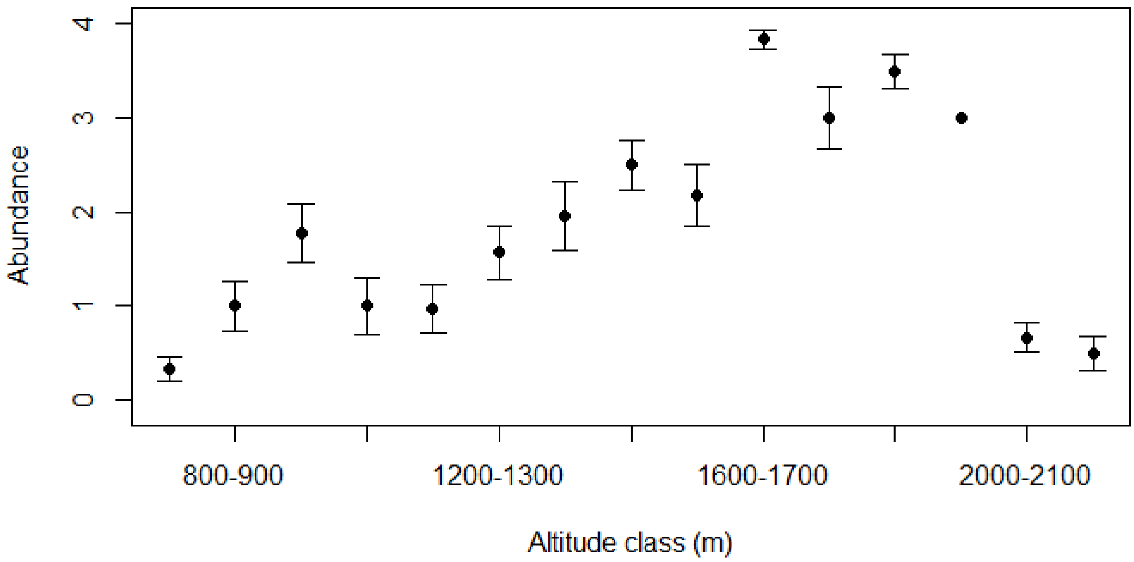

Figure 3. Abundance (mean and standard error) across altitude classes in the study area.

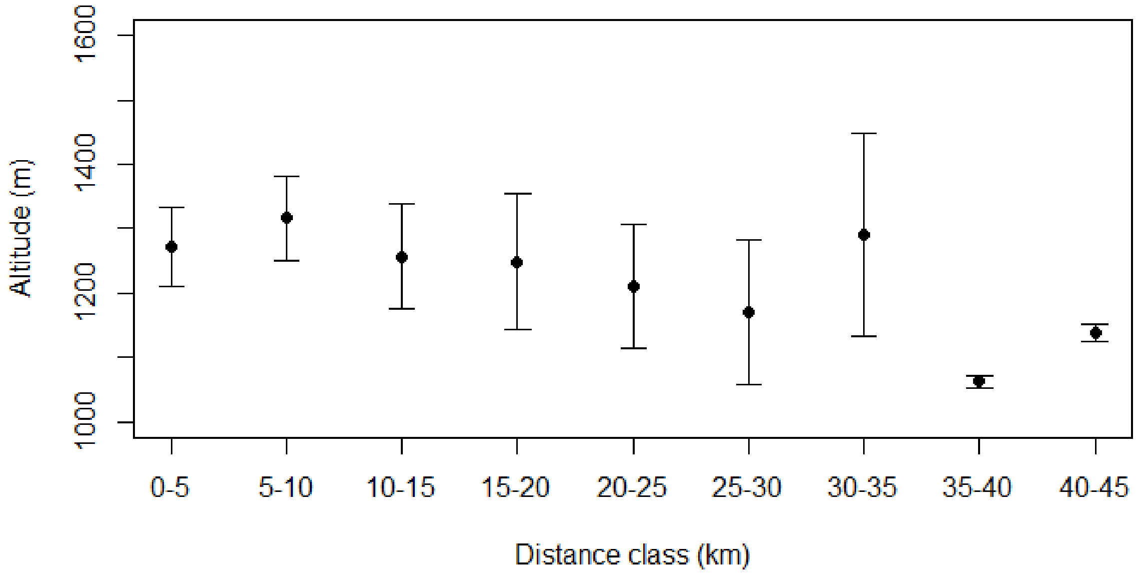

Figure 4. Average altitude (mean and standard error) across distance classes in the study area.

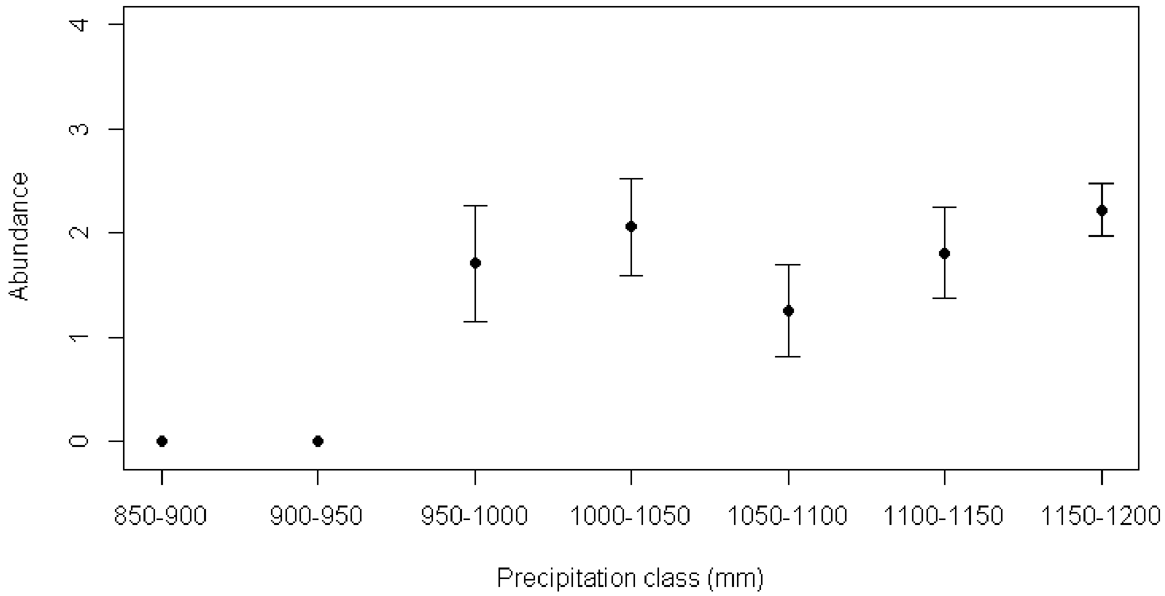

Figure 5. Abundance (mean and standard errors) across precipitation classes in the study area.

Comparing environmental conditions across ranges

Lilium formosanum occurs in areas with very similar values of: annual mean temperature, maximum temperature of the warmest month and minimum temperature of the coldest month in the native range, Australia and South Africa (Fig. 6b, 6c & 6d). Annual precipitation is on average much higher in the native range than in Australia or South Africa (6a). The plant seems to occur at a range of altitudes, in both the native range and invasive range of South Africa (Fig. 6f), while in Australia the plant appears to occur at lower altitude. In the native range and Australia the plant occurs in areas with higher precipitation in the coldest month than in South Africa (Fig. 6e).

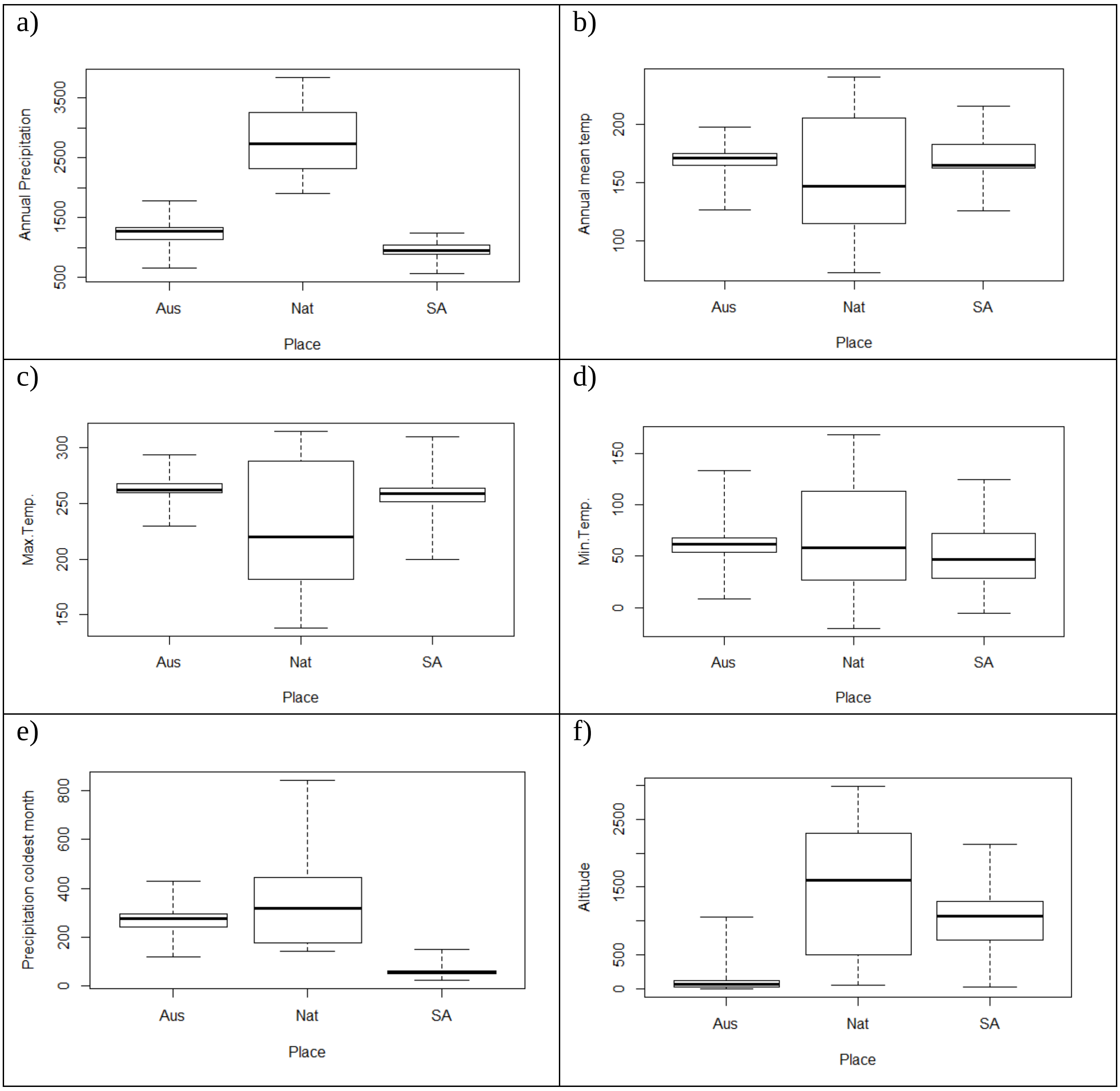

Figure 6. Boxplots showing the range of values experienced by *Lilium formosanum* in its native range (Nat), in Australia (Aus) and South Africa (SA) for a) Annual precipitation (mm), b) Annual mean temperature ($^oCx10$), c) Maximum temperature of warmest month ($^oCx10$), d) Minimum temperature of coldest month ($^oCx10$), e) Precipitation of the coldest month (mm) and f) Altitude (m).

Predicting climatically suitable areas

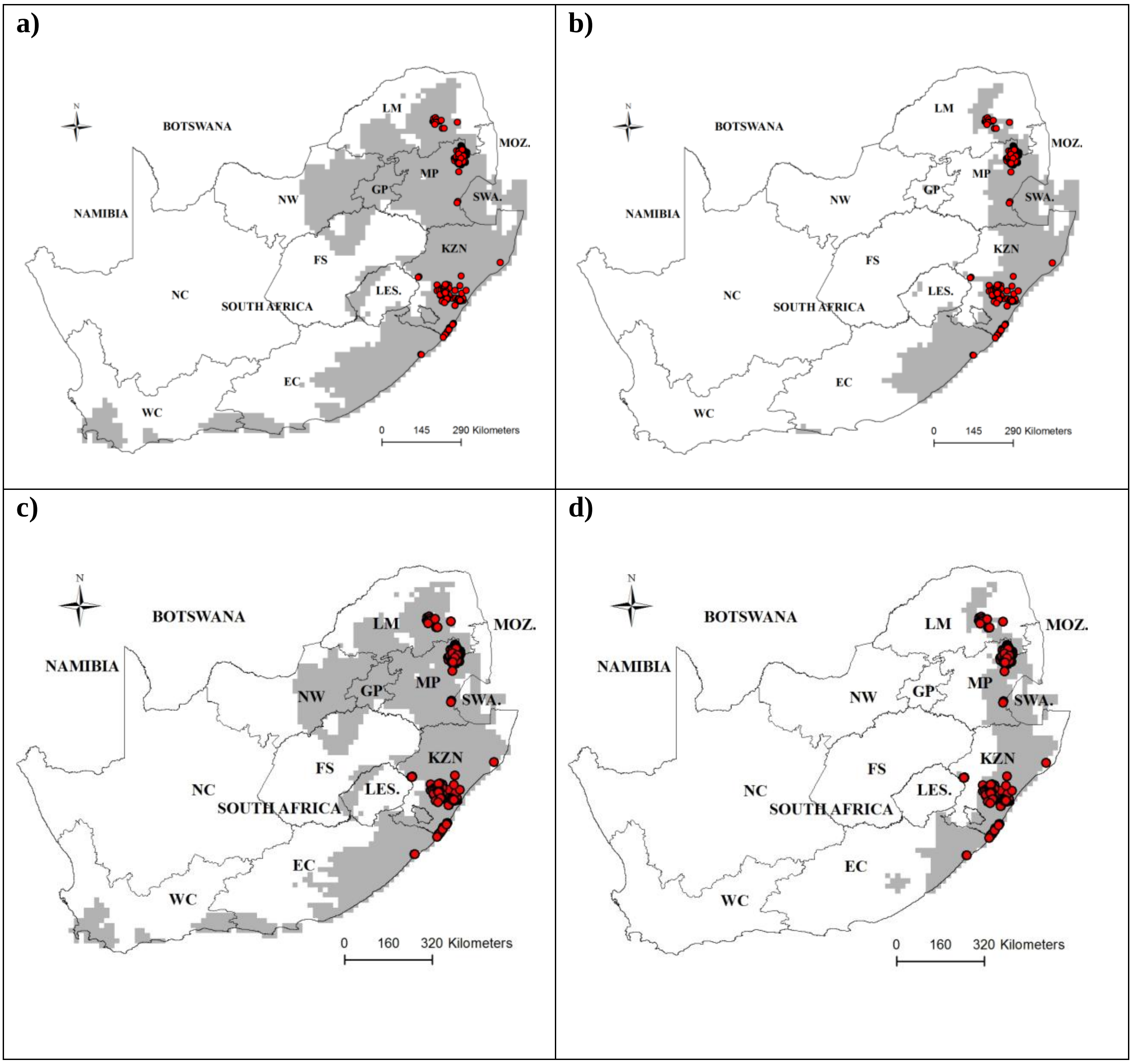

Figure 7. Distribution models for *Lilium formosanum* in southern Africa, developed using the BIOCLIM algorithm and calibrated using: a) all known occurrence records and four predictor variables (Bio1, Bio5, Bio6 and Bio12); b) all known occurrence records and 19 predictor variables; c) South African occurrence records and four predictor variables; d) South African occurrence records and 19 predictor variables. Occurrence records for *Lilium formosanum* in South Africa are indicated with red dots. Countries: LES. – Lesotho; MOZ. – Mozambique; SWA. – Swaziland. South African provinces: LM.–Limpopo; MP. – Mpumalanga; GP. – Gauteng; NW. – North West; KZN. – KwaZulu-Natal; FS. – Free State; EC. – Eastern Cape; NC. – Northern Cape; WC. – Western Cape.

The distribution models for *L. formosanum* predicted the northern and eastern parts of South Africa and the coastal north-east of South Africa as being climatically suitable areas for *L. formosanum* (Fig. 7). The models that predicted the largest regions of southern Africa as being suitable were the those calibrated using all known records and four predictor variables (Fig. 7a) and the model calibrated using South Africa records and four predictor variables (Fig. 7c). These two models showed very similar patterns and the areas that were predicted to be climatically suitable included; the whole of Gauteng, Mpumalanga, KwaZulu-Natal and Swaziland; part of Eastern Cape, Limpopo and North West; and small portions of Western Cape, Free State and Lesotho. The models that were calibrated with 19 predictor variables were much more conservative (Fig. 7b and 7d). These two models also showed very similar patterns of suitability (i.e. Fig. 7d was slightly more conservative than 7b) and areas that were predicted to be suitable included part of Limpopo, large parts of Mpumalanga, Swaziland, KwaZulu-Natal and a small part of Eastern Cape.

Distribution models of *L. formosanum* in the Asian region and Australia show relatively restricted areas that are suitable for *L. formosanum*. The model that predicted the largest region of Asia and Australia as being suitable was the model calibrated using native records and Australian records and four predictor variables (Fig. 8c) and the areas that were predicted suitable included; a large region of China, Indonesian islands, the western part of Australia and part of New Zealand. The model calibrated with Taiwan records only and four predictor variables (Fig. 8a) showed relatively fewer areas of Asia as being suitable and these areas included parts of China and Indonesia. The models that were calibrated with 19 predictor variables were conservative (Fig. 8b and 8d). These two models showed similar patterns of suitability, however the model calibrated using native records only and 19 predictor variables (Fig. 8b) was more conservative than the model calibrated using native records and Australian records and four predictor variables (Fig. 8a), and areas that were predicted suitable included parts of China, Taiwan and Australia. The model calibrated with native records only and 19 predictor variables was more conservative (Fig. 8b). When 19 predictor variables are used to calibrate the model, with Taiwan and Australian occurrence records, very few climatically suitable areas are selected.

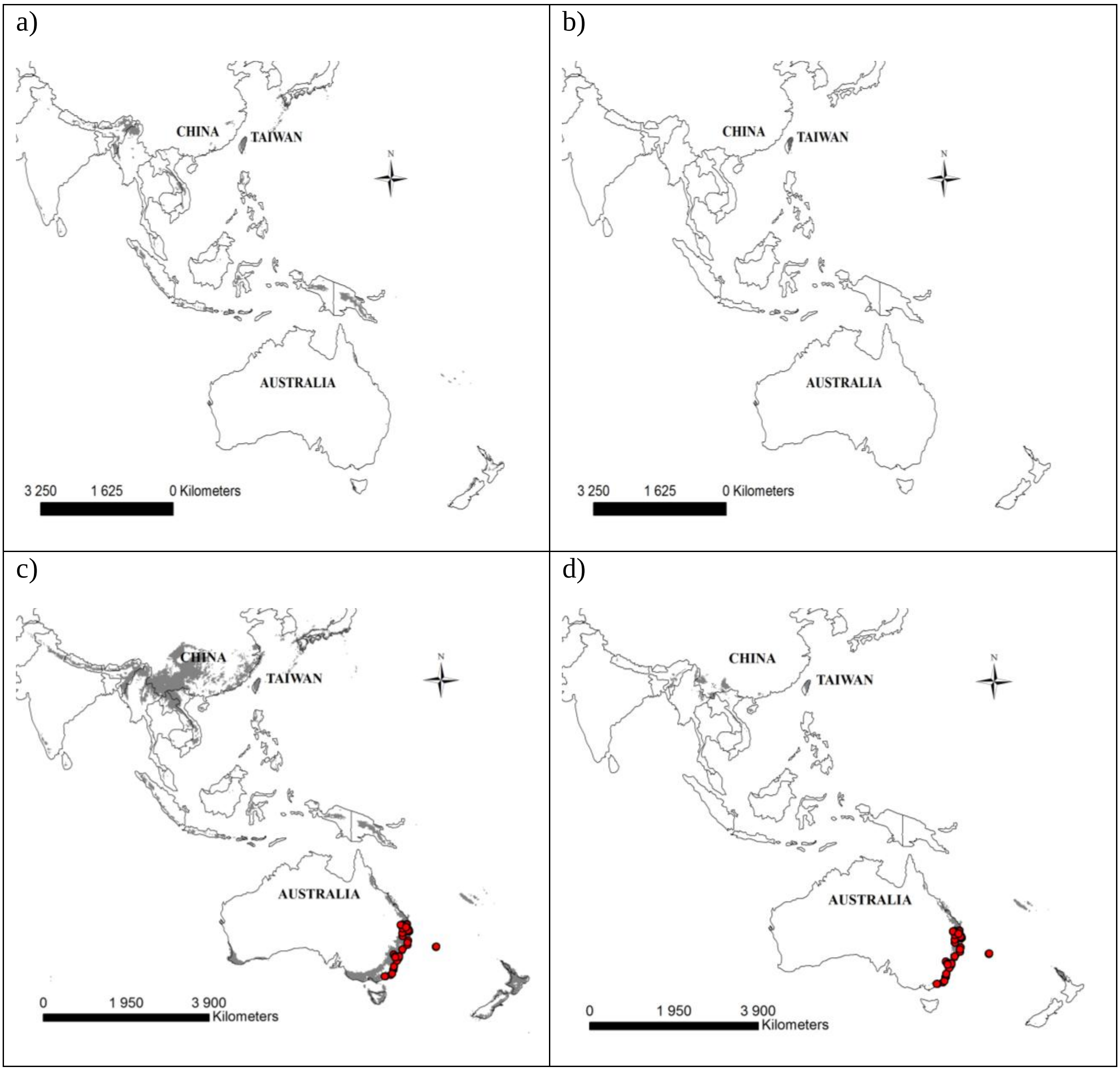

Figure 8. Distribution models of *Lilium formosanum* in Asian region, developed using the BIOCLIM algorithm and calibrated using a) Taiwan occurrence records and four predictor variables (Bio1, Bio5, Bio6, and Bio12); b) Taiwan occurrence records and 19 predictor variables; c) Taiwan occurrence records and Australian occurrence records and four predictor variables; d) Taiwan occurrence records and Australia occurrence records and 19 predictor variables. The darker shading shows areas that are predicted to be climatically suitable for the survival of *Lilium formosanum*

The global distribution model (Fig. 9a) of *L. formosanum* calibrated using four predictor variables and all known occurrence records predicts many regions to be climatically suitable., The model calibrated with 19 predictor variables predicts a much more restricted area of the

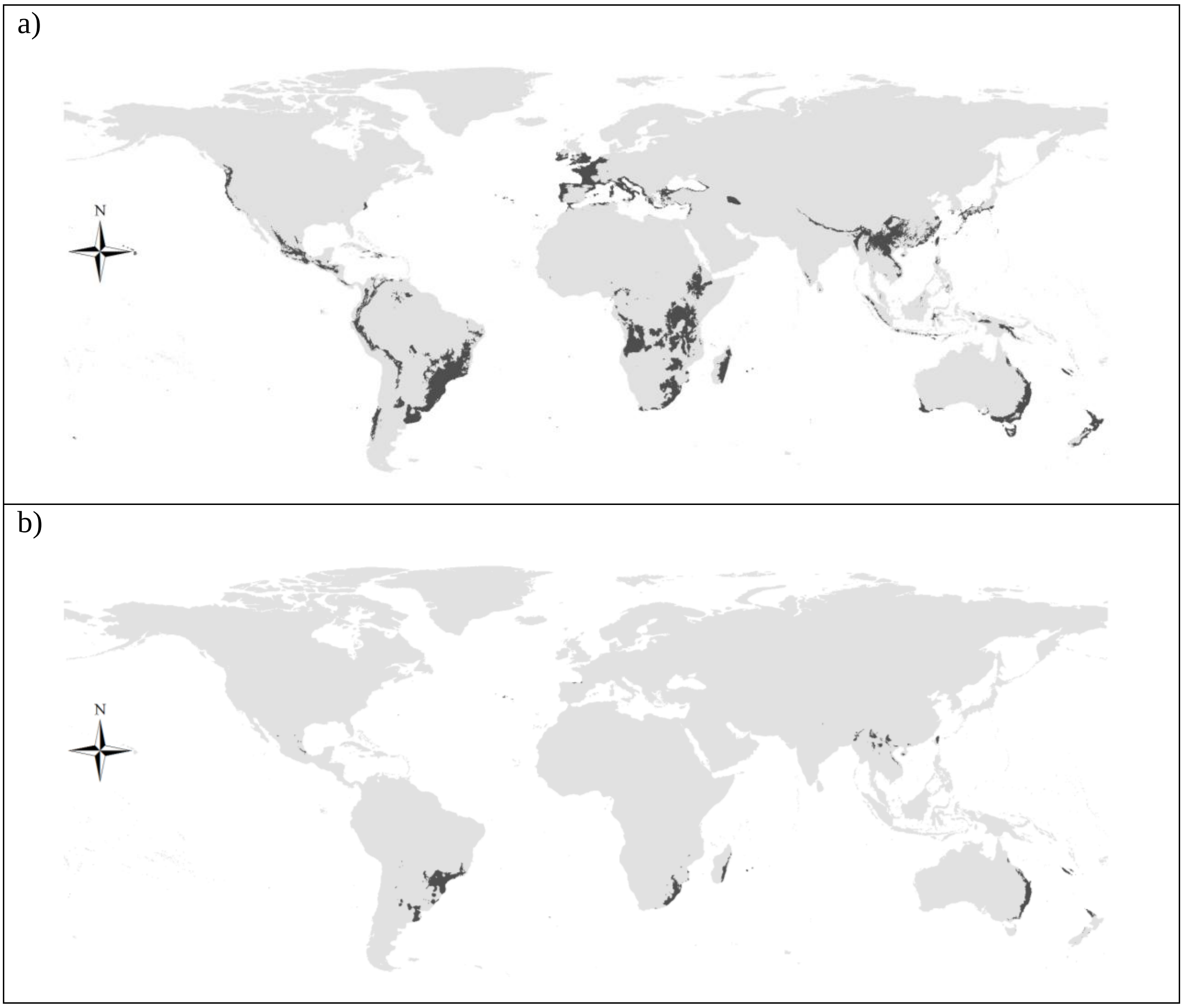

Figure 9. Distribution models for *Lilium formosanum* globally, developed using the BIOCLIM algorithm and calibrated using: a) all known occurrence records and four predictor variables (Bio1, Bio5, Bio6 and Bio12); b) all known occurrence records and 19 predictor variables. The darker shading shows areas that are predicted to be climatically suitable for the survival of *Lilium formosanum*

globe to be suitable for survival of *L. formosanum*. The regions that are predicted climatically suitable include; most parts of central Africa, Eastern parts of Southern Africa, South America and part of western America, Asia, Australia and Switzerland. There are few areas (Fig. 9b) predicted to be climatically suitable for the survival of *L. formosanum*. Fewer suitable areas (darker areas) are predicted when 19 predictor variables were used with all globally known occurrence records and most of these areas correspond with the distribution records of known occurrence used in the model. Regions which are predicted to be climatically suitable (Fig. 9a and 9b) include central Africa, southern Africa, South America, the western part of United States of America, parts of Europe, Asia, Australia and New Zealand.

DISCUSSION

Invasion extent and abundance patterns

The two towns of Sabie and Graskop were suspected to be the source of the invasion of *L. formosanum* in South Africa and the invasion front of the plant was observed to be invading away from the two towns. As one travelled further away on all routes from the two towns, the abundance of *L. formosanum* declined (Fig. 2). Consistent with other studies (Arèvalo *et al*. 2005; Richardson and Pyšek 2006), the invasion pattern of the plant across most routes in the study area did not form a continuous front, rather high population density occurred close to the two towns and decreased as one moved away from the towns. The high abundance close to the two towns was attributed to the assumption that *L. formosanum* invasion spread from the two towns where it was cultivated and is now spreading into natural and disturbed areas along roads. This invasion trend of *L. formosanum* could be a result of suitable habitat and propagule pressure (Rejmànek *et al*. 2005; Catford *et al*. 2011) and the species is likely to spread further in future. Furthermore, abundance patterns from different routes did not have the same patterns. Some routes were found to be more favourable than others for invasion. Some routes were comparatively high in *L. formosanum* abundance, for example the route from Lydenburg to Sabie (R9). Richardson and Pyšek (2006) indicated that fewer propagules were needed in the environment with low resistance for the invasion of any plant to be rapid. Apart from route R9 being more favourable for *L. formosanum* invasion, the high level of abundance could be due to the invasion history of the species and that the species has had insufficient time to attain high densities on all routes. On the other hand, those routes might have high resistance to invasion and as a result high propagule supply would be required for them to fully invade those routes (Rejmànek *et al*. 2005; Richardson and Pyšek 2006).

Predictor variables explaining abundance of *L. formosanum*

Increasing distance from the towns of Graskop and Sabie were expected to have a significant effect on *L. formosanum* abundance. From the model results, the hypothesis was supported, since when distance was the only explanatory variable used (model 1, Table 3) it had a significant effect on *L. formosanum* abundance, which was consistent with the work of Arèvalo *et al.* (2005). However, it was not only distance that had a significant effect on *L.*

formosanum but altitude and annual precipitation influenced of the abundance the species. It seems to be capable of surviving over a considerable altitudinal range. The species grows from low altitude to above 2100 m a.s.l., which is consistent with previous studies on the species (Hiramatsu *et al.* 2001; Wen & Hsiao, 2001). It also survives in a broad range of environmental conditions (Warner *et al.* 2006), since in the native range it grows in relatively high precipitation areas while in its invasive range (South Africa and Australia) it grows in comparatively lower rainfall areas (Fig. 6a) indicating its ability to grow in low rainfall areas. This has important implications for its management in South Africa in order to reduce further spread to other areas around Sabie and Graskop that have not yet been invaded and areas that are currently at low invasion densities could become denser. Since it has broad environmental tolerances, it implies a very proactive eradication or management is required to reduce incursion to other new areas which have not been invaded. Warner *et al.* (2006) highlighted the importance of reducing new establishment through reduction of seed production.

Climatically suitable areas

Areas which are climatically suitable for *L. formosanum* are influenced by the number of occurrence records from the native range and invaded range as well as number of predictor variables used. Hijmans *et al.* (2012) indicated that when few predictor variables were used, larger areas which will be climatically suitable are predicted. Similarly in this study, when all 19 predictor variables were used with any set of occurrence records, fewer climatically suitable areas were selected. Also Beaumont *et al.* (2005) in their study when using all 35 climatic parameters, climatically suitable areas predicted did not even extend past the present distribution of the species. However, when four predictor variables (Bio 1, Bio 4, Bio 5 and Bio 12) which I think are most relevant to *L. formosanum* (based on where it currently grows in South Africa) were selected with any set of occurrence records, a larger climatically suitable area was predicted. The areas predicted to be climatically suitable are consistent with areas which are already heavily invaded by a number of invasive species in South Africa (Henderson 2007; Vardien *et al*. 2012) and they include coastal areas in the Eastern Cape, and KwaZulu-Natal, the interior part of South Africa which include major parts of Limpopo and Mpumalanga in which the species seems to be spreading. For efficient management of invasive species, predicted areas serve as early warning for areas at risk of future invasion by species (Catford *et al.* 2011). For species with invasive potential like *L. formosanum*, the earlier the warning the better chances to contain its spread (Rejmànek *et al.* 2005).

It is possible that greater climatically suitable areas would still have been selected if more occurrence records were used with any set of predictor variables. However, there is a chance that some occurrence records were omitted while cleaning the GBIF records and Australian virtual herbarium (AVH) records. For some of the records from the AVH, it was not clear as to whether the records represented cultivated specimens or were from the natural environment and as a result were excluded. The regions which might be affected by this are the Asian and Australia regions and when predicting globally suitable climatic areas.

CONCLUSION

Lilium formosanum invasion stems from the towns of Sabie and Graskop and follows all routes which originate from the towns. This study revealed the high abundance of *L. formosanum* close to the towns which declined as one moved further away. Distance from the towns therefore appeared to influence the abundance of *L. formosanum*. From the study, annual precipitation was also identified as a factor that could explain the abundance of *L. formosanum* in Mpumalanga, since high abundance of the plant was recorded at areas with high precipitation. Furthermore, climatically suitable areas were identified for large parts of southern Africa, including the northern region of South Africa, the eastern part KwaZulu-Natal coastal belt. Other parts of the world that were predicted suitable included parts of South America, central Africa to Southern Africa, parts of Europe, Asia, Australia and New Zealand.

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Wordclim (Climate data)-http://www.worldclim.org/

APPENDICES

Appendix 1. Altitude class used in the model to determine altitudinal influence on *Lilium formosanum* abundance in the study area.

Class	Altitude range
1	700–1100m
2	1100–1500m
3	1500–1900m
4	1900–2300m

Appendix 2. Annual Precipitation range used in the model to determine precipitation influence on *Lilium formosanum* abundance in the study area.

Class	Annual precipitation range
1	800–1000mm
2	1000–1020mm
3	1020–1060mm
4	1060–1100mm
5	>1100mm

Appendix 3. 19 climatic variables used to determine climatic variables which best explain *Lilium formosanum* abundance in the study area.

Acronym	Description
Bio1	Annual Mean Temperature
Bio2	Mean Monthly Temperature range
Bio3	Isothermality
Bio4	Temperature Seasonality
Bio5	Maximum Temperature of the Warmest Month
Bio6	Minimum Temperature of the coldest month
Bio7	Temperature annual range
Bio8	Mean temperature of the wettest quarter
Bio9	Mean temperature of the driest quarter
Bio10	Mean temperature of the warmest quarter
Bio11	Mean temperature of the coldest quarter
Bio12	Annual precipitation
Bio13	Precipitation of the wettest month
Bio14	Precipitation of the driest month
Bio15	Precipitation seasonality
Bio16	Precipitation of the wettest month
Bio17	Precipitation of the driest month
Bio18	Precipitation of the warmest quarter
Bio19	Precipitation of the coldest quarter