On the distribution and ecology of the African wild silk moth, *Gonometa*

By

Morgan Jade Raath

Submitted in partial fulfilment of the requirements for the degree

Magister Scientae

In the Faculty of Natural and Agricultural Sciences

Department of Plant Science

University of Pretoria

Pretoria

Supervisor: Dr. M. Greve

Co-supervisors: Dr. P.C. le Roux, Dr. R. Veldtman

November 2015

The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF.

DECLARATION

I, ...MORGAN JADE RAATH..........declare that the thesis/dissertation, which I hereby submit for the degree ...MSC (PLANT 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: ...27/11/2015..........

ACKNOWLEDGEMENTS

I would like to thank the following people for the time, help and continual support that they provided me with throughout the course of my study:

Dr. Michelle Greve, Dr. Peter le Roux and Dr. Ruan Veldtman: thank you for your guidance, support, patience, suggestions and comments during the course of the project, and for making this project possible for me. Thank you for your assistance and time during difficult aspects of the project and for believing in me. Thank you also for affording me the opportunity to work with you and to learn from you. You have taught me so much over the past two years and for this, I am extremely grateful.

Prof. Joop Boomker and Dr. Richard Peigler: thank you for your support and willingness to help me. Thank you also for sharing your knowledge on *Gonometa* species with me.

Prof. Gretel van Rooyen, Lizande Kellerman, Nick Wood and Prof. Braam Van Wyk: thank you for your guidance and for taking the time to answer a few questions that I had. Thank you also to Dr. Dino Martins for providing me with information on *Gonometa* host plants.

Dr. Michelle Greve, Isabelle Buyens and Clarence Raath: thank you for your assistance with my fieldwork. I would also like to thank Isabelle Buyens for assisting me with the numerous insect-related questions that I had and for sharing her knowledge with me. Thank you Dr. Michelle Greve, Dr. Peter le Roux and Isabelle Buyens for helping me overcome a few of the obstacles that I faced whilst doing my fieldwork.

Dr. Heather Campbell: thank you for your time and for assisting me with ant species identifications. Thank you for your sharing your expertise with me and for your willingness to answer my questions.

A special thank you to everyone who assisted me in attaining species locality records for my SDM chapter, including the staff at: Afromoths (Jurate and Willie de Prins), the Agricultural Research Council (H. Combrink and V. Uys), Denver Museum of Nature and Science (obtained by Dr. R. Peigler), Ditsong Museum (Martin Kruger), Mississippi Entomological Museum, National Museum of Natural History (Smithsonian Institution), Natural History Museum of Zimbabwe (Ms. D.C. Madamba), Natural History Museum (London) and Oxford University Museum (Dr. J.E. Hogan) for providing me with *Gonometa* species locality records. Thank you also to Dr. W. Mey, Alex Prozorov, H. Staude, M. Ströhle, A. Curle, Joop Boomker, J. Groenewald, and M. Maclean for supplying me with locality records.

Thank you also to members from the Lepidopterists Society (in particular Les Underhill and Martin Hill). Thank you to Jurate and Willie de Prins; Dr. Duncan MacFadyen; Hannelie Mitchell; Jeanene Jessnitz; Prof. S.R. Shaw; A.T. Fombong, Esther Kioko; Dr. R. Oberprieler; Robert White; Evelyn Boswell; Steve Woodall and Alan Heath for guiding me to possible sources of records for the moths.

For *Gonometa* host tree locality records: thank you to Dr. Michelle Greve; Prof. Braam Van Wyk; Elsa Van Wyk; Magda Nel; John Burrows (Buffelskloof Nature Reserve); Mark Hyde; Brenda Daly, Michelle Williams and Elaine Josias (SANBI); Dr. I.J. Kithcing; Sally Fost and Terence Olkers.

My family and friends: thank you for your support and love, and for listening to me talk excitedly (and perhaps too often) about my work. Thank you for your encouragement and for listening to several of my presentations. To my mom and dad, thank you for standing by me and for giving me the opportunity to further my studies. Without you, I would not be where I am today.

Pieter and Tanya Grové at Oppiknoppi Guest Farm: thank you for allowing me to use your farm for my study and for always being so accommodating to us. Thank you also to Pieter and Tanya Grové, Louis Hauman and the other farmers in the Hotazel area and also to Marie Warren, Chrizette Neethling and Duncan MacFadyen (Tswalo Nature Reserve) for keeping an eye out for *G. postica* moths for me and for the constant updates that you gave me.

Thank you to the licensing and permitting authorities, Ms. J. Mans (Department of Agriculture, Fisheries and Forestry) and Ms. M.D. Smit (Department of Environment and Nature Conservation, Kimberly) for issuing my licence (number: NCU 4640714) to use *V. erioloba* and my permits (numbers: FAUNA 424/2/2014, FAUNA: 1736/2014 and FAUNA 1737/2014) to collect and transport biological material.

The University of Pretoria and the Department of Plant Science: thank you for allowing me to use your facilities.

The National Research Foundation (NRF): thank you for the funding that you supplied me over the past two years.

The South African National Biodiversity Institute (SANBI): thank you for the funding that you supplied.

On the distribution and ecology of the African wild silk moth, *Gonometa*

Student: Morgan Jade Raath

Supervisors: Dr. Michelle Greve, Dr. Peter le Roux & Dr. Ruan Veldtman

Department: Plant Science, University of Pretoria

Degree: MSc

ABSTRACT

The African wild silk moths, *Gonometa postica* and *G. rufobrunnea* are a valuable natural resource in southern and East Africa because of the high quality silk fibre derived from their cocoons. However, using these species for commercial silk production has proven problematic because of the sporadic and unpredictable nature of *Gonometa* outbreaks. Moreover, little is known about the ecology and distribution of the *Gonometa* species.

The first part of this study focussed on the importance of moth-host plant interactions, in addition to climatic variables, in determining the species' current regional distributions, using species distribution modelling (SDM). Based on recent studies which have documented the importance of biotic interactions in shaping broad-scale species distributions, I expected moth-host plant interactions to be an important predictor of *Gonometa* species distributions because of the species' dependencies on host plants for survival. Contrary to expectation, my results showed that models' predictive power did not improve following the inclusion of moth-host plant interactions. Biotic and abiotic models predicting *G. postica* distribution performed fairly well, but all models predicting *G. rufobrunnea* distribution performed poorly. Nonetheless, host plant distributions contributed significantly to SDMs of large-scale *Gonometa* distributions, along with annual mean temperature, annual precipitation and precipitation seasonality. Host plant distribution also appeared to limit *Gonometa* species distributions, suggesting that the effect of host tree occurrence patterns on *Gonometa* species distributions should not be ignored. The idea that climate drives large-scale species distributions was supported, but host plant occurrence also had an effect on *Gonometa* species distributions.

The second focus of this study was the potential ecosystem engineering effect created by *G. postica* (via its cocoons) for other invertebrates. Arboreal ants are known to use a wide

variety of plant structures as potential nesting sites, including structures created by arboreal ecosystem engineers. However, ant nest site selection in arboreal systems is poorly understood. I observed, for the first time, ants using empty *G. postica* cocoons as shelter and nesting sites on the myrmecophilic tree *Vachellia erioloba*. I examined cocoon selection by these ants and tested whether selection was based on cocoon characteristics. Cocoons were predominantly occupied by one dominant ant species, but in some cases simultaneously by two ant species. Ant abundance and occurrence were positively related to cocoon size, the presence of scale insects on branches of the trees and cocoon entrance hole type (i.e. cocoons containing only small parasite holes), and negatively influenced by cocoon occupancy by other invertebrates. This suggested that ants select *G. postica* cocoons based on specific cocoon characteristics, and revealed a novel ecological role of the moth-host plant interaction at a local-scale, where the product of this interaction (i.e. cocoon production) appeared to benefit arboreal invertebrates. Empty *G. postica* cocoons probably create a new, favourable habitat for ants. Thus, *G. postica* acts as autogenic ecosystem engineer in arboreal habitats.

This study highlighted the importance of *Gonometa*-host plant interactions in shaping large-scale *Gonometa* species distributions, but also showed that these interactions may play a role in the abundance and distribution of arboreal species at local scales.

Table of Contents

List of tables

Appendices

List of figures

Appendices

CHAPTER 1

Literature review

3.1 INTRODUCTION

African wild silk moths (*Gonometa postica* Walker 1885 and *Gonometa rufobrunnea* Aurivillius 1922: Lasiocampidae) are of great economic interest in their native southern and East African regions (Akai *et al*., 1997; Veldtman *et al*., 2002; Delport, 2006). The elaborate process of metamorphosis from caterpillar to moth results in the production of cocoons which are exploited for their high-quality silk fibre, rivalling that of the domesticated silkworm, *Bombyx mori* (Lepidoptera: Bombycidae) and other indigenous silk moth species (Veldtman *et al*., 2007). In southern Africa, *G. postica* and *G. rufobrunnea* are the only two indigenous moth species currently utilized for commercial silk production (Veldtman *et al*., 2004). They are therefore a valuable natural resource (Veldtman *et al*., 2002) and serve as a promising source of income in southern and East Africa (Freddi *et al*., 1993; Veldtman, 2005).

Gonometa postica larvae are known to forage on a variety of host trees which include their main host trees *Vachellia erioloba*, *Vachellia tortilis*, *Vachellia nilotica* and *Senegalia mellifera*, minor host trees *Senegalia ataxacantha*, *Burkea africana* and *Brachystegia* spp., and even alien host trees, *Acacia mearnsii*, *Acacia elatior* and *Prosopis glandulosa* (Hartland-Rowe, 1992; Veldtman *et al*., 2007; Fening *et al*., 2008; Ngoka *et al*., 2008; Fening *et al*., 2010). *Gonometa rufobrunnea* has mainly been reported to feed on *Colophospermum mopane*, as well as *Brachystegia* species and *Parinari curatellifolia* in southern Africa (Hartland-Rowe, 1992; Kroon, 1999). Current silk harvesting practices are completely reliant on the survival of *Gonometa* pupae and larvae from natural populations that are dependent on the host plants (Veldtman *et al*., 2007). Therefore, due to the trophic connection between *G. postica* and its host plant species (Fening *et al*., 2008; Fening *et al*., 2010) and the potential for this consumer-resource interaction to affect *Gonometa* performance, distributions and responses to climate change (Fening *et al*., 2010; Wisz *et al*., 2013), the significance of the *Gonometa*-host plant interaction for commercial silk production needs to be assessed.

Gonometa rufobrunnea was first identified as a source of wild silk in 1985, which led to the establishment of Shashe Silk Pty (Ltd) in northwest Botswana in 1987 (Hartland-Rowe, 1992). The cocoons of this species were extensively harvested between 1986 and 1987 in Francistown (Botswana) and sold to Shashe Silk (Hartland-Rowe, 1992; Veldtman *et al*., 2002), but this enterprise ended due to a reduction in cocoon abundance as well as a drop in the international silk price. The exact cause of the population crash (i.e. whether it was due to overexploitation of the species or due to natural fluctuations in the species' populations) remains unknown (McGeoch, 2000). Additionally, attempts to rear *G. rufobrunnea* in southern Africa in the past have been unsuccessful (Hartland-Rowe, 1992). *Gonometa* *postica* (Fig. 1.1) serves as an alternate source of high-quality silk, but sustainably harvesting *G. postica* has also proven difficult due to its sporadic and unpredictable population outbreaks and a reduction in populations in countries where it is harvested, (e.g. Kenya; Fening *et al*., 2008). These problems associated with the harvesting of *Gonometa* populations have caused industries such as Shashe Silk to fail (Delport, 2006). Small-scale silk industries have been initiated, but consistent problems faced by these industries include the limited supply of cocoons and unpredictability in the *Gonometa* populations (which fluctuate between high and low densities).

In Kenya the problems encountered by silk industries have been largely avoided through the use of a semi-captive rearing technique, which has been developed and successfully employed here as a small scale industry (Ngoka *et al*., 2008; Fening *et al*., 2008; Fening *et al*., 2010). This approach entails rearing larvae in net sleeves attached to host plant branches containing fresh leaves. However, a major constraint with potential larger scale artificial rearing of these moths is that the moths do not always emergence from cocoons simultaneously (Veldtman, 2005), and as a result, rearing populations that are large enough to meet silk demands is problematic. In contrast, in Ganyesa and Morokweng (North West Province of South Africa), empty (wild) *G. postica* and *G. rufobrunnea* cocoons are currently collected, cleaned and degummed (Veldtman *et al*., 2002; Veldtman *et al*., 2007). However, though this practice of collecting empty cocoons is more sustainable than live harvesting, empty cocoons yield a lower silk quality and value than that of occupied cocoons. This is because empty cocoons are older than occupied cocoons and contain emergence holes. The natural populations of *Gonometa* are therefore faced with extensive potential pressure from illegal harvesting of occupied cocoons, making it possible for this natural resource to be over-exploited (Hartland-Rowe, 1992). Obstacles faced by the silk harvesting industry in the past and at present can be attributed to the lack of understanding of *Gonometa* species' biology (including their behaviour, abundance and ecology), poor management (McGeoch, 2002) and the limited information regarding their distributions in southern Africa (Chikwenhere, 1992; Hartland-Rowe, 1992; Veldtman *et al*., 2007).

This study will therefore examine the role of the abiotic and biotic factors in shaping the distributions of two *Gonometa* species to contribute to the current limited understanding of the geographic ranges of these species. This study is the first to model the distributions of *G. postica* and *G. rufobrunnea*, and will thus also form a part of a foundation towards a broader, long-term goal, which is to implement a sustainable silk harvesting industry in South Africa. Lastly, this study will touch on a previously unstudied aspect of the ecology of *G. postica* by examining the significance of *G. postica* as habitat creators or potential ecosystem engineers (via cocoon production) for ants and other invertebrates associated with its main host tree, *V. erioloba*. Therefore, a better understanding of the consequences of harvesting vacant *G. postica* cocoons will be obtained.

Figure 1.1. *Gonometa postica* (Walker, 1855). Female (left), Male (right). Photograph taken at the Ditsong Museum.

3.2 LITERATURE REVIEW

3.2.1 Gonometa *species biology and utilisation for commercial silk production*

3.2.1.1 Life cycles of G. postica *and* G. rufobrunnea

Gonometa species have been extensively harvested despite the fact that little is known about their biology (Veldtman *et al*., 2002). An aspect of *Gonometa* biology that is known is the identity of their host plants, because host plants are a central component of the life cycles of these moths (Hartland-Rowe, 1992; Fening *et al*., 2008; Fening *et al*., 2010). Virtually all known host plants for *G. postica* in southern Africa are woody trees belonging to the legume family. Major host trees, which include *Vachellia erioloba*, *Vachellia nilotica, Vachellia tortilis* and *Senegalia mellifera,* and minor host trees including *Vachellia karroo, Senegalia ataxacantha* and *Burkea africana,* are the main food sources for the moth in the Kalahari region (Hartland-Rowe, 1992; Veldtman *et al*., 2007; Fening *et al*., 2008; Ngoka *et al*., 2008; Fening *et al*., 2010). Some of these tree species also our in East Africa, where *G. postica* has also been reported. *Gonometa rufobrunnea* forages mainly on *Colophospermum mopane,* which occurs in western, southern Africa, whereas in East Africa, *G. rufobrunnea* forages on *Brahystegia spicifomis* and *Parinari curatellifolia* (Hartland-Rowe, 1992; Kroon, 1999). Only the *Gonometa* larval stages feed − primarily on the leaves of host plants (Hartland-Rowe, 1992). Because the larvae are relatively sedentary while feeding, and only move away from the feeding site to pupate during their final instar stage, they are completely reliant on the host tree on which the parent oviposits to develop, grow and survive (i.e. to successfully transition through life stages and complete their life cycles). However, studies focussed on the *Gonometa*-host plant interactions (e.g. Fening *et al*., 2008; Fening *et al*., 2010), i.e. *Gonometa* performance on host plants and their preferences for certain host plants over others, are limited. *Gonometa* species appear to display preferences for certain host trees over others, even when multiple host tree species are present in an area (personal observation; Fening *et al*., 2008); however, the reason for this is unknown. Moth development time and cocoon size and weight (i.e. moth performance) also vary between host tree species (Ngoka *et al*., 2008; Fening *et al*., 2010).

Moreover *G. postica* and *G. rufobrunnea* have been found to co-exist on host trees, and although hybrids of the moths have been identified in the past, all were identified to be male and inactive, weighing half of that of the parent individuals (Hartlan-Rowe, 1992). These hybrids also produced thin, papery cocoons. Some experts believe that *G. rufobunnea* is a subspecies of *G. postica;* however, these species can be distinguished from one another at almost every stage of their life cycles (Hartland-Rowe, 1992). Further work is required on *Gonometa* species genetics to delimit their taxonomies.

To my knowledge, only one study (i.e. Delport, 2006) has addressed *G. postica* population genetics, by examining genetic connectivity between eruptions both within and between years and by assessing the relationship between population size fluctuations and genetic structure in southern Africa. They observed a high degree of spatial and temporal variability in *G. postica* populations, with extensive dispersal of the species across South Africa. Moreover, microsatellite loci developed for *G. postica* revealed gene flow levels to be high. When dispersal is high, population size fluctuations (which are characteristic of *Gonometa* species) could have a homogenising effect on spatial genetic pattern because of the population connectivity and genetic drift (Delport, 2006). Other aspects of *Gonometa* species biology that have been documented are the development of these moths and their morphology (Hartland-Rowe, 1992; Ngoka *et al*., 2008).

The life cycle of *G. postica* and *G. rufobrunnea* is complex, characterised by two generations per year in southern and East Africa (Delport, 2006; Veldtman *et al*., 2007; Fening, 2008; Ngoka *et al*., 2008; Fening *et al*., 2009; Fening *et al*., 2010), one with and the other without diapause (Hartland-Rowe, 1992; Ngoka *et al*., 2008). The first generation is initiated in early spring (September), when adults emerge from cocoons (Veldtman *et al*., 2007; Ngoka *et al*., 2008). Adults do not feed because they lack feeding mouthparts

(Hartland-Rowe, 1992), and adult females are short-lived (surviving for approximately a week post-emergence) with limited flight ability (Veldtman *et al*., 2007). Mating therefore occurs within 24 hours of emergence (pers. comm. Ruan Veldtman), and the pro-ovigenic females lay their eggs in clumps (of 2-25 eggs) over a period of four to five days or longer. Females lay between 150 and 200 eggs (pers. comm. Ruan Veldtman; Hartland-Rowe, 1992), and after approximately two weeks, the eggs hatch and the first generation larvae feed and develop on host plants for two months. The larvae are gregarious up until the third instar (Ngoka *et al*., 2008) and feed only at night (Hartland-Rowe, 1992). The sixth and final instar larvae of *G. postica* have contrasting white, black and brown colouration which makes them highly visible on their host plants (Veldtman *et al*., 2007). Pupation occurs again in November-December and varying proportions of these larvae undergo rapid development. New adults (second generation) emerge in mid-summer (December-January). Males start spinning their cocoons earlier than females, but all moths emerge simultaneously (Ngoka *et al*., 2008). These individuals and the remaining un-emerged first generation pupae enter diapause. They overwinter and emerge the following spring.

Despite this available knowledge on *Gonometa* species biology, their use for commercial silk production remains a challenge.

3.2.1.2 Use of Gonometa s*pecies for silk harvesting*

There are three means by which *G. postica* and *G. rufobrunnea* are currently used for silk production in southern and East Africa (Veldtman, 2005), and the success of these techniques mediates the efficiency with which *G. postica* and *G. rufobrunnea* can be collected and therefore their potential to be exploited sustainably for economic benefit (Veldtman, 2005; Ferguson & Wilson, 2011). These techniques are: harvesting natural populations, artificial rearing of eggs to the pupal stages, and seeding or mass release of individuals into natural areas. Usually, cocoons are collected from the wild, mainly during seasons when rainfall is reliable and when cocoons are available (Fening, 2008). They are then used to breed *Gonometa* larvae semi-captively. Alternatively, because of the unpredictable nature of *Gonometa* population outbreaks, empty cocoons are used for silk harvesting (Veldtman, 2005; Veldtman *et al*., 2007). Although this practice does not appear to detrimentally affect *Gonometa* populations, cocoon availability may be limited.

Seeding, which is a hybrid method between artificial rearing and natural harvesting, has been tested at every stage of *G. rufobrunnea*'s life cycle (Hartland-Rowe, 1992). It is a moderately successful technique for establishing *Gonometa* populations in areas where they are absent or where their densities are low. The least successful technique is seeding of adult moths, possibly due to the emerged moths being exposed to unnatural conditions (Hartland-Rowe, 1992). In contrast, cocoon seeding, which is currently the most studied method, has proven effective in producing new populations. Egg seeding, which proved to be ineffective initially, can result in the production of a small number of cocoons (Hartland-Rowe, 1992). A much greater success rate has been observed when eggs have been seeded on trees within net-sleeve cages (similar to the semi-captive rearing technique applied in Kenya (see Ngoka *et al*., 2008)). These net sleeves are advantageous because they protect *Gonometa* species from predators, parasites and other natural enemies, thus increasing *Gonometa* survival and productivity (Ngoka *et al*., 2008).

Each of these methods has their own set of disadvantages. For example, harvesting of natural populations is only viable when *Gonometa* populations reach high densities. Due to the high spatial and temporal variability of *Gonometa* species populations (Veldtman *et al*., 2007), natural harvesting is therefore unlikely provide a continuous, predictable cocoon supply. A major constraint of artificial rearing of *Gonometa* species is that there is limited knowledge relating to how larvae grow in response to host plant quality (Veldtman, 2005). Moreover, these species are difficult to rear in captivity, and synchronisation of moth emergence is needed to ensure mating success and the generation of a large enough population for sustainable silk production. Seeding of *Gonometa* species is disadvantageous in that late instar mortality is a problem due to parasitoids and predators (Hartland-Rowe, 1992).

Until more knowledge is available on the population dynamics and ecology of *Gonometa*, i.e. how their populations are affected by both biotic and abiotic factors and the scales at which these factors operate, the only alternatives for silk industries are to continue harvesting and degumming empty cocoons or to look into improving seeding and artificial rearing techniques. Identifying the main drivers of *Gonometa* distributions may provide silk industries with a starting point towards locating potential outbreak areas and, more generally, an improved understanding of the species' ecology. For this reason, this study first examines the role of abiotic and biotic factors in shaping *Gonometa* species distributions, by specifically looking at the importance of the *Gonometa*-host plant interaction in shaping their distributions at a large scale (relative to abiotic factors).

3.2.2 Gonometa *species distributions: the importance of the moth-host plant interaction*

3.2.2.1 Gonometa *population dynamics and outbreaks*

Data on insect population dynamics in southern Africa are limited with the two extremes of these dynamics being "latent" and "eruptive" (McGeoch, 2002; Veldtman *et al*., 2007). The population dynamics of *G. postica* and *G. rufobrunnea* have not been extensively studied (Veldtman *et al*., 2004); however, their populations are reported to occupy an intermediate position on the gradient from latent to eruptive, and display large inter-annual fluctuations in population size over different spatial and temporal scales (Veldtman, 2005; Delport, 2006; Veldtman *et al*., 2007). Such fluctuations are characteristic of many moth species (e.g. Alalouini *et al*., 2013; Tamburini *et al*., 2013) and can be attributed to both density-dependent factors (i.e. presence of host trees, predators, parasitoids, bacteria and viruses), or density independent factors (i.e. climate).

One aspect of insect population dynamics which remains a challenge is understanding the factors that cause insect outbreaks (Maron *et al*., 2001; Turchin *et al*., 2003; Veldtman, 2005; Abbott & Dwyer, 2007; Nelson *et al*., 2013). Such is the case for *Gonometa* species, for which it is unclear whether population eruptions occur after populations are exposed to ideal conditions or if eruptions are initiated through the dispersal of individuals that belonged to previously eruptive populations (Delport, 2006). Eruptions have been observed following periods of drought; it is suggested that this is because drought conditions are unfavourable for larval parasites (Hartland-Rowe, 1992). In contrast, periods of heavy rainfall have been observed to result in large population crashes through early instar mortality.

Numerous factors have been proposed as explanations for variation in the timing and duration of outbreaks in other insect species, all of which can be linked to population fluctuations (Maron *et al*., 2001). These factors, which may interact to cause population eruptions (Turchin *et al*., 2003; Ferguson & Wilson, 2011) include favourable climatic conditions, food limitation and quality, disease and trophic interactions such as competition, parasitism and predation between insects and plants (Liebhold *et al*., 2000; Maron *et al*., 2001; Williams & Liebhold, 2002; Turchin *et al*., 2003; Abbott & Dwyer, 2007; Klemola *et al*., 2010; Alalouini *et al*., 2013; Nelson *et al*., 2013).

Gonometa populations can reach very high densities over large areas during outbreak periods, which can result in massive host tree defoliation, tree growth reduction or tree mortality (Lovett *et al*., 2002). For this reason, the impact of climate and biotic factors on

Gonometa populations are important aspects to address, as they provide us with a stepping stone towards understanding eruptive populations.

3.2.2.2 Possible factors driving Gonometa *species distributions*

The biotic and abiotic factors affecting species population dynamics, which include climate, host plant density, habitat structure, dispersal characteristics of the species, escape from natural enemies and species interactions (Veldtman *et al*. 2007), have the ability to influence species behaviour and microhabitat preference, and could also scale up to drive species distributions (Roland, 1993; Guido & Gianelle, 2001; Martin, 2001; Arab & Costa-Leonardo, 2005; Ritchie *et al*., 2009; Van der Putten *et al*., 2010; Boulangeat *et al*., 2012). The effects of these biotic and abiotic factors on species and their distributions vary between herbivore species with different life histories (Bale *et al*., 2002; Veldtman *et al*. 2007). To understand species population dynamics and species habitat requirements, identification of these environmental factors and determining how they relate to species' life histories, is important. *Gonometa postica* and *G. rufobrunnea* are examples of species that differ in their life history traits and defence traits (such as aggregation behaviour and colouration), and host specificity (Veldtman, 2005; Veldtman *et al*., 2007). It is therefore expected that their distribution patterns could differ.

Furthermore, individuals within a species that are at different life stages are faced with different factors that influence survival and selection. Various mortality factors are at work throughout the life cycle of *Gonometa* species, which vary in space, time and intensity, and may therefore contribute to the patchy distribution patterns observed in the species (Hartland-Rowe, 1992). Studies have shown the spatially and temporally patchy distribution of *Gonometa* populations to be correlated with climatic variables (Veldtman, 2005; Delport, 2006), with temperature and relative humidity influencing *Gonometa* developmental period (Fening *et al*., 2010). Not only are climatic factors important for timing of moth emergence (or outbreak initiation), but they also play a role in regulating the timing of food availability (Hartland-Rowe, 1992). Therefore, climate may indirectly affect herbivore abundances and distributions via its effect on host plants, which results in bottom-up trophic cascades (Wright, 1983).

A major biotic factor that could mediate herbivore distributions is the distribution of their host plants, the effects of which are likely to vary between specialist and generalist herbivores (Kelley & Farrell, 1998; Östergård & Ehrlén, 2005; Ali & Agrawal, 2012). This poses a question on the importance of biotic interactions versus climate in shaping *Gonometa* species distributions. Moreover, in East Africa and South Africa, there are several wasps and flies that parasitize *G. postica* larvae (Fening *et al*., 2009; Veldtman *et al*., 2004). Therefore, parasitoids may have a greater effect on *Gonometa* populations than climate, and could restrict *Gonometa* distributions. Parasites have also been found to regulate the population dynamics of other Lepidoptera (Gould *et al*., 1990; Berryman, 1996; Zhou *et al*., 2001; Klemola *et al*., 2010; Klemola *et al*., 2014). Separating the effects of biotic and abiotic factors on species distributions is a challenge in ecology (Hawkins *et al*., 2003). However, developments in the field of species distribution modelling (Guisan & Thuiller, 2005; Elith & Leathwick, 2009) – from the early 1920s, where correlations were made between species distributions and climate, to the mid-1970s which marked the development of computer-based modelling techniques; and advances in statistical and computer sciences in the 1980's that led to the development of the informative tools that we have today (Guisan & Thuiller, 2005) – have enabled us to untangle their relative contributions to *Gonometa* distributions.

3.2.2.3 Species distribution modelling

Species distribution models (SDMs) are tools which make use of georeferenced species locality data (in the form of presence, presence-absence or abundance data) and an array of environmental predictor variables (which are assumed to affect species eco-physiology and resource assimilation abilities) to estimate the potential distributions of species using various statistical methods (Guisan & Thuiller, 2005; Elith & Leathwick, 2009). They are fundamental tools in applied research in biogeography (Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Kearney & Porter, 2009) and have applications in ecology, conservation science and evolution (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith *et al*., 2006). However several challenges are associated with their use (Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Jiménez-Valverde *et al*., 2008), including data sampling design and model building, parameterization strategies and model selection and evaluation strategies. Some of these challenges have been addressed through developments within this field; but, theoretical limitations remain due to the lack of integration of ecological theory associated with SDMs (Austin, 2002; Guisan & Thuiller, 2005; Soberón, 2007).

Numerous tools (Elith *et al*., 2006; Hernandez *et al*., 2006; Phillips *et al*., 2006; Phillips & Dudík, 2008, Elith *et al*., 2011) and methods (Kissling *et al*., 2012) are available for modelling species distributions. Maxent, which is amongst one of the best performing SDM methods, was used here. It models species distributions using presence-only data and can utilise categorical and continuous data (Phillips *et al*., 2006; Elith *et al*., 2011). The ability to model distributions using presence-only data is beneficial because databases frequently contain only presence data. Furthermore, Maxent is not sensitive to sample size (Elith *et al*., 2006; Hernandez *et al*., 2006), which is advantageous because often occurrence data are limited for modelling species distributions.

One of the major criticisms of SDMs, regardless of the tools or methods used, relates to the niche concept (Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Kearney, 2006; Soberón, 2007; Jiménez-Valverde *et al*., 2008), on which they are reliant (Guisan & Zimmermann, 2000; Wiens *et al*., 2009). Niche differences could result in the observed geographic patterns through space because species range limits are mediated by a set of biotic and abiotic conditions that delimits its niche. In the early 1900s, the Grinellian and Huchinsonian niche concepts were developed (Guisan & Zimmermann, 2000; Pulliam, 2000; Wiens *et al*., 2009). The former defines a species' niche as fundamental, where species are thought to occupy all potential suitable areas (i.e. abiotic conditions limit a species); whereas, the latter considers species occupancy to be as we observe it in nature (i.e. realized), where biotic interactions exclude species from part of their fundamental niche (Pulliam, 2000; Kearney, 2006; Jiménez-Valverde *et al*., 2008). The realized and fundamental niches of species thus differ fundamentally. Such ambiguities in what defines the niche of a species have led to conflicting views about what SDMs actually represent (Araújo & Guisan, 2006; Kearney, 2006). Early approaches for modelling species distributions have mainly involved bioclimatic envelope modelling, which only considers the effects of climatic variables on species distributions (Pearson & Dawson, 2003; Boulangeat *et al*., 2012) and ignores the effects of processes such as dispersal and biotic interactions. These models may explain climate-based variance in species occurrence patterns, but predictors such as resource distribution and other biotic interactions which may be key in determining the distribution of the species are ignored (Guisan & Thuiller, 2005). Therefore, recent reconsiderations of the niche concept, the development of niche theory and how it relates to species distributions has inspired the inclusion of important parameters such as dispersal, physiology and biotic interactions (which include competition, predation, host-parasite interactions, facilitation, mutualisms and consumer-resource interactions) into the modelling process (Carey, 1996; Bascompte, 2009; Elith & Leathwick, 2009; Kearney & Porter, 2009; Bateman *et al*., 2012; Wisz *et al*., 2013).

Another main challenge with SDMs relates to scale, and which variables are important at what scales for shaping species distributions (Pearson & Dawson, 2003; Elith & Leathwick, 2009; Wisz *et al*., 2013). Pearson and Dawson (2003) provide a conceptual, hierarchical framework relating to the influence of predictors of species distributions at different scales. They suggest that climate is the main factor diving species distributions at broad (e.g. continental) scales, while topography and land cover play a role at local scales. Biotic interactions and microclimate are considered to be important further down this hierarchy (at finer scales). However, more recently, several studies have documented the importance of biotic interactions in shaping species distributions at broad scales (Araújo & Luoto, 2007; Brooker *et al.,* 2007; Heikkinen *et al.*, 2007; Gilman *et al.*, 2010; Meier *et al.*, 2010; Schweiger *et al.*, 2012; Wisz *et al.*, 2013), indicating that their impacts on species distributions extend beyond local extents. This warrants the inclusion of biotic interactions and testing if biotic interactions improve SDMs, which have previously been largely ignored in SDMs.

Furthermore, developments in fine scale climate change data in the past few years have allowed for SDM studies to investigate the effect of climate change on species distributions (Guisan & Thuiller, 2005; Thuiller *et al*., 2005; Beaumont *et al*., 2002). Species can either shift their distributions through adaptation to new environments, remain isolated in refugia, or become extinct in response to climate change (Warren *et al*., 2001; Bale *et al*., 2002; Thuiller *et al*., 2005; Araújo *et al*., 2004; Parmesan, 2006; Keppel *et al*., 2012). These three changes, which have been observed for some herbivorous species (Bale *et al*., 2002; Schweiger *et al*., 2008), are expected for *G. postica* and *G. rufobrunnea*. Moreover, climate can alter species interactions (including *Gonometa*-host plant interactions) and therefore also indirectly influence species' geographic ranges into the future via changes in nature and/or the outcome of biotic interactions (Hughes, 2000; Blois *et al*., 2013). Overlaps between interacting species can be reduced or eliminated through shifts in species' phenologies or via changes in species traits in response to climate change (Stefanescu *et al*., 2003; Menéndez, 2007; Jamieson *et al*., 2012; Schweiger *et al*., 2012). Including biotic interactions into the modelling process may therefore yield more accurate results and more realistic estimations of predicted suitable areas for species into the future, than if these are excluded (Austin, 2002).

Thus, the first component of this thesis uses an SDM approach to model the southern and East African distribution of two *Gonometa* species using 1) only abiotic predictor variables, and 2) modelled host plant distributions along with abiotic variables as predictors, thus incorporating the moth-host plant interaction into the models. Host plant distributions are expected to play a role in shaping *Gonometa* species distributions at a broad scale.

3.2.3 *Cocoons as engineered structures: a valuable product of the* **Gonometa**-*host plant interaction for arboreal invertebrates*

Gonometa postica’s interactions with its host plants may also play an important role at a local scale, particularly for other invertebrates. After moth (or parasitoid) emergence, cocoons may remain on tree branches for quite some time (personal observation). Vacant *G. postica* cocoons may therefore promote a multitude of species interactions within arboreal systems depending on the potential benefits that they provide to these species.

In southern Africa, *V. erioloba* is one of *G. postica*’s main host plants (Hartland-Rowe, 1992; Veldtman *et al*., 2007). These plants can host an array of species, which interact (positively or negatively) with one another and with the plant (Davison & McKey, 1993; Bronstein, 1998; Heil & McKey, 2003; Palmer, 2003; Raine *et al*., 2004; Styrsky & Eubanks, 2007; Blatrix *et al*., 2009; Heil *et al*., 2009; Rosumek *et al*., 2009; Palmer *et al*., 2010; Kaminski *et al*., 2010; Kaminski & Roderigues, 2011; Stanton & Palmer, 2011; Bächtold *et al*., 2014; Mayer *et al*., 2014; Styrsky, 2014). The organisms involved may even exploit other species interactions; for example, orb-web spiders are known to exploit acacia-ant mutualisms for protection against natural enemies (Heil *et al*., 2009; Kaminski *et al*., 2010; Styrsky, 2014). Interactions within these systems can therefore involve three or more trophic levels and consequently lead to top-down and bottom-up trophic cascades (Pace *et al*., 1999; Schmitz *et al*., 2000; Kagata & Ohgushi, 2006).

In ecology, a primary goal is to understand interactions among species, their strength within food webs and the role that they play in shaping ecological communities (Bruno *et al*., 2003; Tirado & Pugnaire, 2005; Agosta, 2006). These interactions along with abiotic environmental constraints, affect species’ habitat choices and niche dimensions (Jeffries & Lawton 1984; Palmer, 2003), and can therefore mediate species co-existence (Soliveres *et al*., 2015). Sometimes species’ habitat choices are mediated by the presence of specialised structures within an environment, such as the thorn and leaf domatia of plants in plant-ant mutualisms (Vasconcelos, 1991; Stapley, 1998; Campbell *et al*., 2013b; Mayer *et al*., 2014), which are usually selected by organisms based on the functions that they provide. For example, species may search out microsites providing shelter, favourable conditions for the individuals and their brood and refuge from hash environmental conditions and natural enemies (Banschbach *et al*., 1997; Fukui, 2001; Stachowicz, 2001). These nesting sites may also be selected based on their characteristics (Thomas, 2002; Campbell *et al*., 2013b), or based on their proximity to food sources (such as honey-dew producing scale insects) (Blüthgen *et al*., 2004). Furthermore, organisms may create nesting sites for themselves

(Edwards *et al*., 2009) or utilise structures created by other organisms within the trees (Tanaka *et al*., 2010) through what is termed ecosystem engineering (Jones *et al*., 1994; Jones *et al*., 1997; Breitburg *et al*., 2010).

Ecosystem engineers make an environment more favourable for themselves or other organisms with which they interact (Jones *et al*., 1994; Jones *et al*., 1997; Breitburg *et al*., 2010), either directly, by reducing abiotic stress, or indirectly, by providing an escape from predators or competitors (Fukui, 2001; Stachowicz, 2001). They can be allogenic where structural changes are caused by the engineers in an environment; or autogenic (accidental), where an environment is modified via the organism's own physical structure (Jones *et al*., 1997; Dangerfield *et al*., 1998; Gutiérrez *et al*., 2003; Jones *et al*., 2006). In both cases, the engineer causes a change in the abiotic environment.

Of the multiple species interactions occurring between species living on *V. erioloba* (Fig. 1.2), the second component of this study will focus on the interaction between *G. postica* and the organisms inhabiting its old cocoons (i.e. acacia ants and other invertebrates). The effect of scale insect presence will also be examined because of their function as a key resource to arboreal ants (Blüthgen *et al*., 2004). Interestingly, despite ants potentially benefitting from the presence of cocoons, ants have exhibited aggression towards *G. postica* on *V. erioloba*, where the ants have been observed to remove *G. postica* larvae from the trees (see Campbell *et al*., 2013a). However, these ants also appear to secondarily utilise empty *G. postica* cocoons as possible nesting sites or protected microhabitats (Fig. 1.3) − similar to the function of the thorn domatia within the trees. *Gonometa postica* is therefore potentially acting as an accidental or autogenic ecosystem engineer (Jouquet *et al*., 2006) for the ants that remove their larvae from trees, and for invertebrates on *V. erioloba*, which is comparable to other arboreal ecosystem engineers (Martinsen *et al*., 2000; Fukui, 2001; Lill & Marquis, 2004; Lima *et al*., 2013).

Empty *G. postica* cocoons persist for extended periods within the trees. Therefore, the engineering effect created by *G. postica* could contribute towards mediating species occurrence on *V. erioloba* (Hastings *et al*., 2007), because the habitats that cocoons provide increase tree structural complexity (Lill & Marquis, 2003). Interactions between ants and other Lepidoptera, which range from obligate-mutualistic and facultative-mutualistic to parasitic, have been widely documented particularly for the butterfly families Lycaenidae and Roidiniae (Fiedler & Maschwitz, 1989; Pierce, 1995; Fiedler, 2006; Kaminski *et al*., 2010; Witek *et al*., 2010; Martins *et al*., 2013); however, no studies have reported the secondary use of Lepidopteran cocoons by ants as nesting sites. Moreover, ant nest site selection and coexistence within myrmecophytes (i.e. ant plants) based domatia or nest morphology is not well established, with most studies examining domatia or nest characteristics (e.g. Leroy *et al*., 2010), and fewer studies linking these characteristics to ant utilization (Stanton *et al*., 1999).

Therefore, in the second part of this thesis, I will investigate whether ants and other invertebrates are using *G. postica* cocoons as nesting sites, and test whether ant abundance and presence in *G. postica* cocoons is influenced by cocoon characteristics. From this, I will be able to determine if ants are selecting *G. postica* cocoons as nesting sites based on cocoon morphology. Species co-occupancy within trees and cocoons will also be examined to test if *G. postica* is acting as an ecosystem engineer for the ants and other invertebrates at local scale. This component will also consider the potential implications of the created ecosystem engineering effect by *G. postica* (via its cocoons) for silk harvesting practices which are reliant on the collection of empty cocoons.

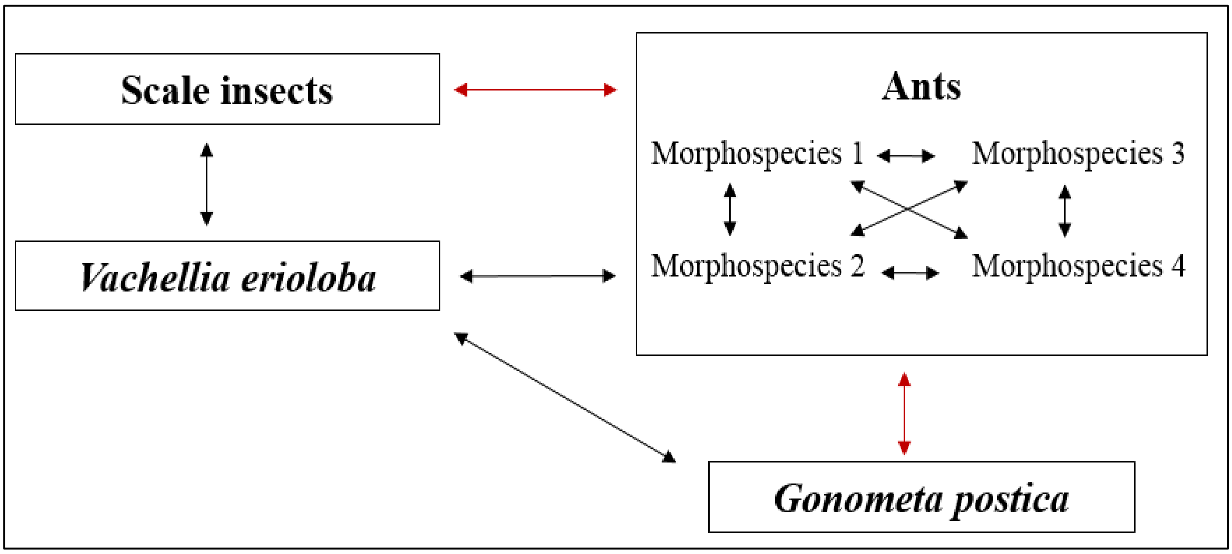


Figure 1.2. Interactions of a number of insects including *Gonometa postica* on *Vachellia erioloba*. The interactions represented in red will be the focus of this study component.

Figure 1.3. An emerged *Gonometa postica* cocoon and associated ants on *Vachellia erioloba*. Scale insects are also visible on the stem beneath the cocoons. Photograph: Isabelle Buyens.

CHAPTER 2

Incorporating biotic interactions into species distribution models: including host plant distributions in distribution models of two African *Gonometa* species

4.1 INTRODUCTION

Species distribution models (SDMs) are the most widely used tools for modelling species distributions (Guisan & Thuiller, 2005; Elith & Graham, 2009; Elith & Leathwick, 2009). SDMs utilise georeferenced species occurrence data in conjunction with multiple environmental variables to predict potentially suitable areas for individual species (Barry & Elith, 2006; Graham *et al*., 2008; Elith & Leathwick, 2009; Elith & Franklin, 2013). However, SDMs typically model species distributions based only on abiotic factors (usually climatic variables alone), and often overlook the role of biotic interactions and dispersal in shaping distributions, particularly at broad scales (Guisan *et al*., 2006; Wisz *et al*., 2013). The few studies that have examined the influence of biotic interactions on species distributions and richness patterns at broad scales have consistently shown the importance of explicitly considering inter-specific interactions such as consumer-resource interactions, facilitation and competition (Araújo & Luoto, 2007; Brooker *et al*., 2007; Heikkinen *et al*., 2007; Gilman *et al*., 2010; Meier *et al*., 2010; Bateman *et al*., 2012; Boulangeat *et al*., 2012;; Schweiger *et al*., 2012; Wisz *et al*., 2013).

Biotic interactions structure the realised niche of species (Araújo & Guisan, 2006; Godsoe & Harmon, 2012), and may therefore strongly influence species distributions (Leathwick & Austin, 2001; Araujo & Luoto, 2007; Schweiger *et al*., 2008; Meier *et al*., 2010), either limiting or expanding the conditions under which a species occurs. Moreover, the impact of a biotic interaction on species distributions can vary considerably across space and time, and may often be species specific (Meier *et al*., 2010; Schweiger *et al*., 2012; le Roux *et al*., 2012; Eskildsen *et al*., 2013) and contingent on environmental conditions (Meier *et al*., 2011). Furthermore, the cascading effects of climate on plant distributions, and plant species distributions on their associated fauna (Wright, 1983), are difficult to untangle. It is the variability in the impacts of biotic interactions, both within and across trophic levels, which has made incorporating these interactions into species distribution modelling difficult (Wisz *et al*., 2013). Nevertheless, biotic interactions may have important implications for predicting species distributions because they can influence species-climate relationships and also shape species distributions beyond local extents (Schweiger *et al*., 2012; Wisz *et al*., 2013). Including interactions into the modelling process is expected to lead to more accurate SDM predictions (Austin, 2002) because potentially important aspects of species distributions, which are not as easily represented by large-scale abiotic predictors (Meier *et al*., 2010), are incorporated into models by the explicit incorporation of biotic interactions.

Incorporating biotic interactions into SDMs might be especially valuable for understanding range shifts under climate change scenarios, because in standard SDMs it is assumed that biotic interactions remain constant and are not important for predicting future species distributions (Guisan & Thuiller, 2005). However, robust predictions of the effects of future climate change on species distributions likely require the consideration of biotic interactions and how their nature and impacts will change (Gilman *et al*., 2010). For example, if interacting species respond to climate change individually, current species interactions could change in the future (Pearson & Dawson, 2003). This could prove detrimental to species that are limited by species that they interact with, such as their host plants, because climate change could increase the number of mismatches between them depending on the species' characteristics and their degree of specialization (Stefanscu *et al*., 2011; Schweiger *et al*., 2012). Species may also migrate at different speeds and in different directions with climate change (Chen *et al*., 2011); therefore, biotic interactions can complicate species responses to climate change and can also interact with the rate of climate change (Brooker *et al*., 2007; Gilman *et al*., 2010). By excluding biotic interactions from the modelling process, SDMs would be unable to predict these shifts in species distributional ranges accurately. Thus, biotic interactions have important implications for assessments on the impacts of climate change on species distributions (Araújo & Luoto, 2007; Gilman *et al*., 2010).

Several approaches have been used to model biotic interactions, mainly at local scales (Kissling *et al*., 2012), and the most widely used approach involves adding the occurrence of purportedly interacting species as a proxy for actual interactions (or by adding the cover or abundance of a species as a proxy for the intensity or frequency of an interaction). Therefore, the known distribution of one species can be used as a predictor of another species' distribution (see Araujo & Luoto, 2007; Heikkinen *et al*., 2007). A related approach is to use abiotic variables to model the distributions of interacting species individually, and then to restrict the distribution of the one species to the modelled distribution of the other species (Schweiger *et al*., 2008). Biotic interactions have also been incorporated into SDMs by combining classic SDM approaches with process-based models (for example, modelling physiological representations of resource competition and bioclimatic limits). With all of these approaches, the effects of biotic interactions on species distributions have frequently been limited to investigating the effect of a single species or the influence of one type of interaction (Van der Putten *et al*., 2010). The more novel approaches for SDM involve incorporating biotic interactions into models within multispecies systems (Kissling *et al*., 2012); however, this kind of modelling requires detailed knowledge of all interactions, which may not always be available.

Previous studies have demonstrated that SDM predictions improve when biotic interactions are incorporated into models (Araújo & Luoto, 2007; Meier *et al*., 2010; Bateman *et al*., 2012), and they may improve the confidence for predicting the impacts of future climate change on species distributions (Brooker *et al*., 2007). Studies that incorporated biotic interactions to model species responses to climate change scenarios have included competition and facilitation into models (Van der Putten *et al*., 2010), but studies involving species interacting with their food sources are limited (Bateman *et al*., 2012). For Lepidoptera, the importance of consumer-resource interactions in shaping species distributions has been documented, in which host plant distributions have been recognised as key predictor variables (i.e. Araújo & Luoto, 2007; Preston *et al.*, 2008).

This chapter examines current and future predicted distributions of two African silk moth species, predicted using only climatic variables (abiotic predictors), and using both climate variables and the occurrence of host tree species as a proxy for the moth-host plant interactions (i.e. abiotic and biotic predictors). *Gonometa postica* Walker 1855 and *Gonometa rufobrunnea* Aurivillius 1922 are of great economic interest due to the high-quality silk derived from their cocoons (Akai *et al*., 1997; Veldtman *et al*., 2002; Veldtman *et al*., 2004; Delport, 2006). *Gonometa postica* is known feed on several host tree species, mainly *Vachellia erioloba*, *Vachellia tortilis*, *Vachellia nilotica* and *Senagalia mellifera* in southern and East Africa. However, *G. postica* has also been reported on *Senegalia ataxacantha*, *Senegalia brevispica*, *Capparis tomentosa*, *Burkea africana* and *Brachystegia* spp., and on the alien tree species *Acacia mearnsii*, *Acacia elatior*, *Acacia nubica*, *Acacia hockii* and *Prosopis glandulosa* (Hartland-Rowe, 1992; Veldtman *et al*., 2007; Fening *et al*., 2008; Fening *et al*., 2010). *Gonometa rufobrunnea*, which has been less well-studied, forages mainly on *Colophospermum mopane* (Hartland-Rowe, 1992), although other host tree species such as *Parinari curatellifolia* and *Brachystegia* spp. have also been reported (Kroon, 1999). The southern African distributions of many of these host trees fairly well-known; however, elsewhere, *Gonometa* distributions remain poorly understood.

In southern Africa, *G. postica* and *G. rufobunnea* have two generations per year coinciding with rainfall seasonality (Hartland-Rowe, 1992). It is therefore expected that temperature and precipitation will have an effect on *Gonometa* distribution, which is in line with other SDM studies on Lepidoptera (see Beaumont & Hughes, 2002; Tóth *et al*., 2013). It is also expected that host tree distributions (i.e. biotic predictors) will play a role in shaping *Gonometa* distributions, as observed for other Lepidoptera (Araújo & Luoto, 2007; Preston *et al*., 2008), because *Gonometa* species are largely dependent on their host plants for the completion of their life cycles (Hartland-Rowe, 1992; Fening *et al*., 2008; Fening *et al*., 2010).

Gonometa species exhibit large inter-annual population fluctuations, and outbreaks or eruptions of these moths are patchily distributed (Veldtman *et al*., 2007), and vary across space (both locally and regionally) and time in southern Africa. As a result of the unpredictable nature of these populations and the limited information regarding *Gonometa* biology, ecology and distribution, the consistent limited cocoon supply has caused silk industries to fail. These problems associated with the use of African wild silk moths by silk industries in southern Africa may be further exacerbated through climate change because changes in temperature and rainfall regimes may affect *Gonometa* species eruptions and their overall distribution (Hartland-Rowe, 1992; Veldtman, 2005). There is thus a need to understand the effects of the exogenous and endogenous factors on *Gonometa* populations to determine whether or not the use of their cocoons for silk industries in southern Africa will be sustainable (Delport, 2006).

4.2 CHAPTER AIMS

The aim of this chapter is to evaluate the role of the moth-host plant interaction in shaping *Gonometa* distributions. This study, being the first to model the southern and East African distributions of *G. postica* and *G. rufobrunnea*, will incorporate biotic (moth-host plant) interactions into the models along with a suite of environmental predictors, thereby potentially increasing the predictive power of the models (Boulangeat *et al*., 2012; Wisz *et al*., 2013). My objectives are:

1. to determine which regions of southern Africa have high and low probabilities of suitable conditions for the *Gonometa* species, thus allowing us to estimate their potential ranges.
2. to determine which environmental variables are the best predictors of host plant and *Gonometa* species distributions.
3. to determine the importance of biotic interactions in shaping *Gonometa* species distributions – i.e. is model performance and predictive power improved when biotic interactions are incorporated into the SDMs?
4. to evaluate the impact of climate change on the distribution of both *Gonometa* species.

4.3 DATA AND METHODS

4.3.1 *Study species*

The distributions of *Gonometa postica* and *G. rufobrunnea* are poorly known (Chikwenhere, 1992; Hartland-Rowe, 1992; Veldtman *et al*., 2007). The main *G. postica* host plant in South Africa is *V. erioloba*. Other host plants include *V. tortilis*, *S. mellifera* and *B. africana*. These acacias occupy dry savannas, whereas *B. africana* is more common within moist savannas (Huntley & Walker, 1982).

Gonometa rufobrunnea forages predominantly on *C. mopane* which occupies the dry savannas in southern Africa (Huntley & Walker, 1982). Other plants such as *Brachystegia* species have also been reported as hosts for *G. rufobrunnea* (Kroon, 1999). In this study, only *B. spiciformis* was used additionally to *C. mopane* because it may be an important host for *G. rufobrunnea* in East Africa (Kroon, 1999) where *C. mopane*, the most commonly reported host plant of *G. rufobrunnea*, does not occur.

4.3.2 *Locality records*

The majority of the locality records of *G. postica* (n = 302) and *G. rufobrunnea* (n = 89) individuals were obtained from museums, private collections and the literature (Table 2.1). Additional records were obtained from personal observations made by amateur lepidopterists and through the use of specimen collection labels. These sample sizes are good based on previous studies conducted in MaxEnt (Hernanez *et al*., 2006; Wisz *et al*., 2008). The locality records show *G. postica* to be distributed over large areas of southern Africa extending across South Africa northwards into Botswana, Namibia, Zimbabwe, Tanzania and Kenya (Fig. 2.1). *Gonometa rufobrunnea* is distributed in the northern parts of the Limpopo Province (South Africa), extending into Botswana and Zimbabwe (Fig. 2.1). The species also occurs in Malawi, parts of Zambia and the Democratic Republic of the Congo, Tanzania, Kenya, Rwanda and Burundi.

The locality records for the host trees of *G. rufobrunnea*, *C. mopane* (n = 830) and *B. spiciformis* (n = 410); and for the host trees of *G. postica*, *V. erioloba* (n = 1277), *B. africana* (n = 1052), *S. mellifera* (n = 1396), and *V. tortilis* (n = 1372) were obtained from databases and herbaria (Table 2.1; Fig. 2.2). Where co-ordinates were not supplied, locality records for both moths and host trees were geo-referenced using the gazetteer ACME Mapper 2.1.

Table 2.1. Main sources of locality records for *Gonometa postica*, *Gonometa rufobrunnea* and their host plants. The number of records per source are indicated in brackets

***Gonometa* species records**

Museums	Private collections	Literature	Personal observations
Afromoths (n = 6)	Mey, W. (n = 28)	Aurivillius (1927) (n = 6)	Barker, C. (n = 1)
Denver Museum of Nature and Science (n = 2)	Prozorov, A. (n = 8)	Campbell *et al.* (2013a) (n = 1)	Bhekisisa (n = 1)
Ditsong Museum (n = 122)	Staude, H. (n = 93)	Fenning *et al.* (2008, 2009, 2010, 2011) (n = 2)	Boomker, J. (n = 1)
Mississippi Entomological Museum (n = 3)	Ströhle, M. (n = 7)	Kioko *et al.* (2000) (n =3)	Curle, A. (n = 4)
National Museum of Natural History(n = 2)		Ngoka *et al.* (2008) (n = 4)	Dreyer, A. (n = 1)
Natural History Museum of Zimbabwe (n = 55)		Raine *et al.* (2011) (n = 1)	Groenewald, J. (n = 1)
Natural History Museum (London) (n = 4)		Taylor (1969) (n = 4)	Heath, A. (n = 2)
Oxford University Museum (n = 2)		Veldtman *et al.* (2002, 2004, 2005, 2007) (n = 12)	Louis, J. (n = 1)
			Maclean, M. (n = 1)
			Raath, M. (n = 9)
			Rebelo, T (n =1)

Host tree records

Databases	Herbaria
GBIF (www.gbif.org) (n = 751)	H.G.W.J. Schweickerdt Herbarium (n = 27)
Flora of Zimbabwe (www.zimbabweflora.co.zw) (n = 490)	Buffelskloof Nature Reserve Herbarium (n = 6)
PRECIS (SANBI) (n =364)	
Flora of Namibia (www.nbri.org.na) (n = 442)	
Greve *et al.* (2012) (n = 4258)	

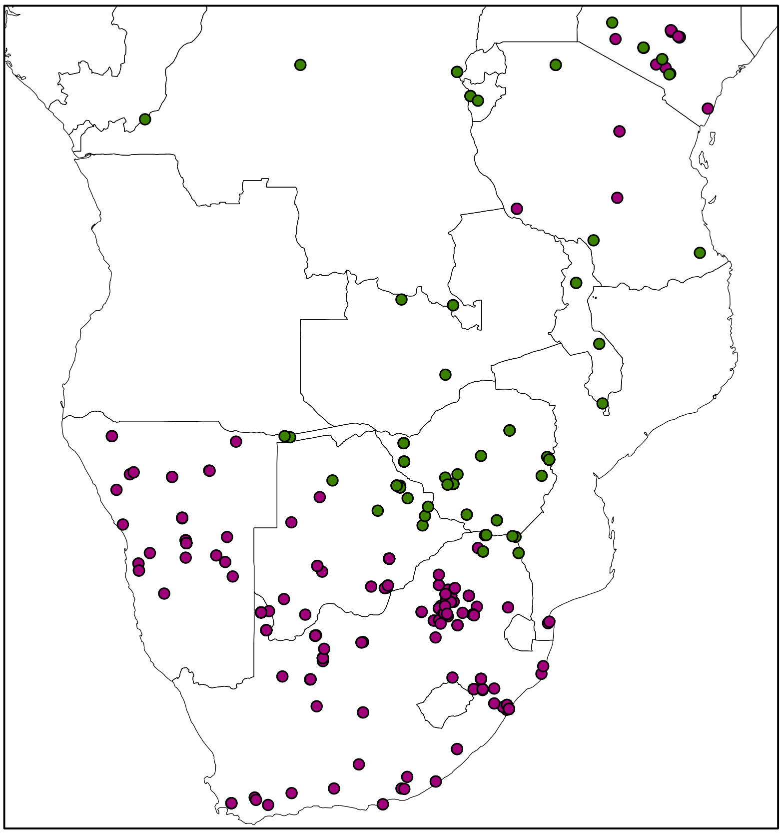


Figure 2.1. Locality records for *Gonometa postica* (purple) and *Gonometa rufobrunnea* (green) in southern and East Africa.

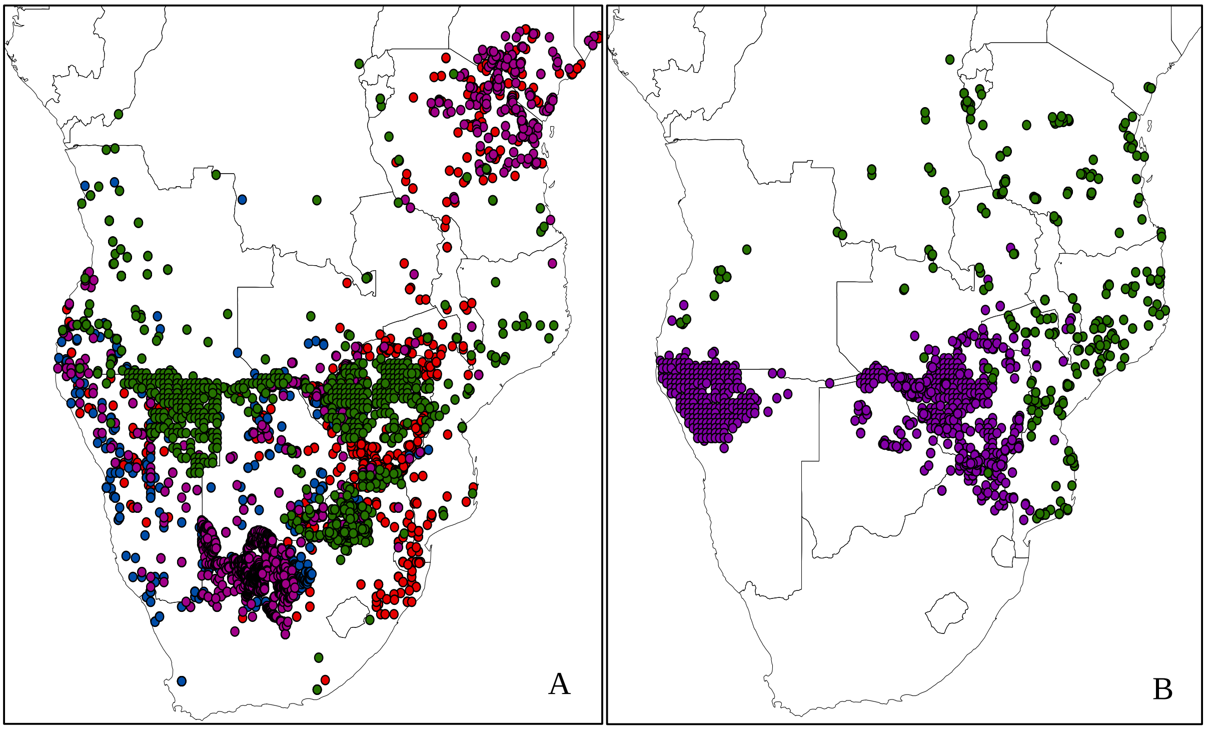


Figure 2.2. A) Locality records for *Gonometa postica* host plants. Green: *Burkea africana*, red: *Vachellia tortilis*, blue: *Vachellia erioloba*, purple: *Senegalia mellifera* B) Locality records for *Gonometa rufobrunnea* host plants. Purple: *Colophospermum mopane*, green: *Brachystegia spiciformis*.

4.3.3 *Environmental predictor variables*

Climate data were downloaded from the Worldclim database (Hijmans *et al*., 2005) at 2.5-min spatial resolution for annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), mean temperature of the driest quarter (BIO9), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of the driest quarter (BIO17) and precipitation of the coldest quarter (BIO19). BIO9 and BIO19 were subsequently removed because of their high correlation ($R^2 > 0.8$) with BIO1 and BIO17 respectively. Additional soil data, including soil organic carbon content, pH, cation exchange capacity, percentage sand content and bulk density were obtained from the SoilGrids database, downloaded at 1 km spatial resolution (Hengl *et al*., 2014). These soil variables did not display high collinearity.

To model the effect of climate change on the distributions of the *Gonometa* species and their host plants, the Woldclim 2070 projections for the five bioclimatic variables were also downloaded (Hijmans *et al*., 2005). A key component for assessing the impact of climate change on species distributions using SDMs involves the use of future climate change scenarios or representative concentration pathways (RCPs). These RCPs, presented in the IPPCs fifth assessment (IPCC, 2014), have been developed to describe different greenhouse gas concentration scenarios and are used to simulate future climate change using Atmosphere-Ocean Global Circulation Models (AOGCMs) and Earth System Models (ESMs) (Baek *et al*., 2013). They represent some of the major driving forces of climate change, including the processes involved, the impacts (ecological, physical and socio-economic) and the potential responses which may be important when informing climate change policy. For the present study, two greenhouse gas emission scenarios (RCP 4.5 and RCP 6) were selected to assess potential future distribution of the moth species. Both RCP 4.5 and RCP 6 project an eventual stabilization of anthropogenic radiative forcing levels after 2100. RCP 4.5 predicts stabilization to 4.5W/m^2 (approximately 650 ppm CO_2) after 2100, and RCP 6 predicts stabilization to 6 W/m^2 (approximately 850 ppm CO_2) after 2100 (Van Vuuren *et al*., 2011).

The projections from two general circulation models (GCMs), HadGEM2-ES and IPSL-CM5A-LR, were used. Variations of the Hadley model have been used widely in the literature for modelling species distributions in southern Africa (Erasmus *et al*., 2002; Midgley *et al*., 2003; Tadross *et al*., 2005; Lumsden *et al*., 2009; Midgley & Thuiller, 2011; James *et al*., 2014). HadGEM2-ES is a coupled atmosphere-ocean GCM representing interactive land and ocean carbon cycles and vegetation dynamics (Jones *et al*., 2011). Also included in this model is an interactive tropospheric chemistry scheme which simulates interactions with atmospheric aerosols and the evolution of atmospheric composition. The IPSL-CM5 model incorporates five component models representing the earth system and its carbon cycle (atmosphere, ocean and sea ice, vegetation and continental surfaces and atmospheric chemistry) (Dufresne *et al*., 2013). It was selected due to its good performance in projecting temperature and precipitation in southern Africa (see Ringler *et al*. 2010), although rainfall projections have higher uncertainty than projections for temperature.

All of the environmental layers were in the WGS 1984 projection. The soil layers were resampled to 2.5 min spatial resolution. All layers were clipped to the same extent. Layers were all converted into Ascii files for use in Maxent. These analyses were conducted in ArcMap 10.1.

4.3.4 *Modelling and model evaluation*

Species distribution modelling was conducted across southern and East Africa (south of the equator) using a maximum entropy approach in Maxent (Phillips *et al*., 2006). Initially, the current and future (2070) potential distributions of *G. postica* and *G. rufobrunnea* were modelled using only the climatic variables (hereafter referred to as "Abiotic models"; Fig. 2.3). These variables were selected based on the seasonal nature of *Gonometa* species' outbreaks and their sensitivity to rainfall and drought periods (Hartland-Rowe, 1992; Delport, 2006).

A second set of models was run to predict *Gonometa* distributions that incorporated moth-host plant interactions into the models. To do this, the distributions of the host plants *V. erioloba*, *S. mellifera*, *V. tortilis* and *B. africana* (for *G. postica*) and *C. mopane* and *B. spiciformis* (for *G. rufobrunnea*) were initially modelled in Maxent for the current and future predicted climate. Host tree SDMs were performed using the five bioclimatic and five soil variables as predictors. Soil predictors were included in the models because they play an important role in the distribution of savanna trees. Arid and moist savannas differ substantially in terms of their soil conditions (Huntley & Walker, 1982), which vary in texture and elemental composition, and soil fertility (nutrient content) could play a role in shaping savanna tree distributions. Furthermore, temperature and water availability are considered important drivers of savanna tree distributions (Huntley & Walker, 1982; Smith & Goodman, 1986). Four different maps of host plant distributions were generated from these models which were each used along with the climatic variables (listed above) as predictors of *Gonometa* species distributions, thus incorporating the moth-host plant interactions in the models. Therefore, four different models incorporating host plant maps (hereafter referred to as Biotic 1, Biotic 2, Biotic 3 and Biotic 4) were run to predict each of the *Gonometa* species' distributions (Fig. 2.3).

In Biotic 1, probability distribution maps of each host plant (attained as an output in Maxent) were used along with the climatic variables as predictors of *Gonometa* species distributions. For Biotic 2, presence-absence maps of individual host plant distributions were used along with climatic data as predictors of *Gonometa* distribution. Presence-absence maps were generated by specifying a threshold "equate entropy of thresholded and original distributions threshold" to the probability maps of host plant distributions. This threshold, which may over-predict potential species ranges (Worth *et al.*, 2014), but is less restrictive compared to other thresholds (Morán-Ordóñez *et al.*, 2012) and in this study, showed the best performance compared to other thresholds. For Biotic 3, the generated presence-absence maps of all host plants of *Gonometa* species were combined into a single map of host plant distribution per *Gonometa* species. This map was used along with climatic variables to model the *Gonometa* species distributions. A similar approach was used for Biotic 4; except, the probability maps of the respective host plant distributions of each *Gonometa* species were combined across the study region.

For all models (host tree, *Gonometa* biotic and abiotic), presence localities were divided into random test (20%) and training (80%) datasets to evaluate model accuracy using the area under the receiver operating curve (AUC). These AUC value represent the ability of a model to discriminate between areas where a species is predicted to be present and those where it is predicted to be absent (Hanley & McNeil, 1982). The maximum number of background points was specified to be 5000. To account for the effects of sampling bias for the models predicting *Gonometa* species distributions, pseudo-absences were chosen from the locality records for all Lepidoptera in southern and East Africa, downloaded from GBIF (Elith & Leathwick, 2007; Barbet-Massin *et al.*, 2012). These pseudo-absence data were selected because biases for southern and East Africa Lepidoptera might be a good proxy for sampling biases in *Gonometa*. These data serve as a comparative dataset under which species occurrences in areas can be contrasted to areas where the species are absent (VanDerWal *et al.*, 2009). The locality records for acacias in southern Africa (taken from the database of Greve *et al.* (2012)) were used to account for sampling bias in the host tree distribution models. Presence-absence maps for the modelled predicted distributions were generated using the "equate entropy of thresholded and original distributions threshold" (Phillips *et al.*, 2006).

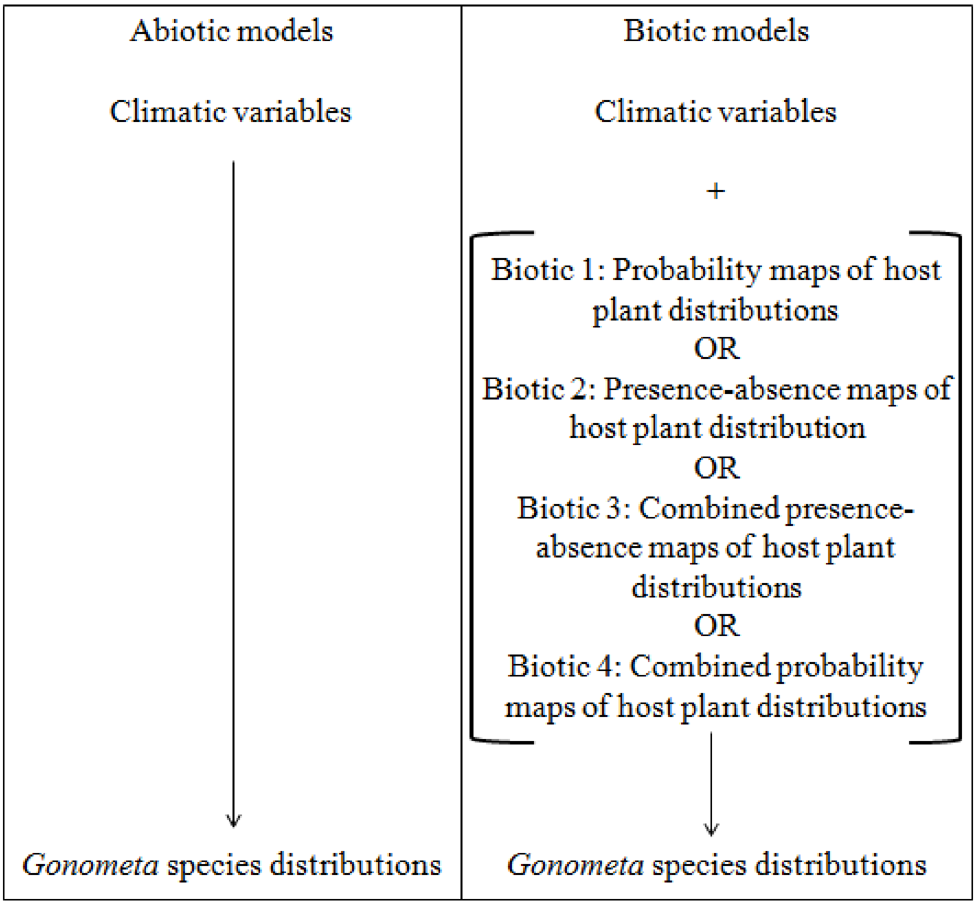


Figure 2.3. Diagram illustrating the different types of models run to predict *Gonometa* species distributions.

4.4 RESULTS

4.4.1 *Model performance and current predicted distribution of Gonometa species*

Out of the different models run to predict *Gonometa* species distributions, the abiotic models and only the two best performing biotic models (Biotic 1 and 4 for *G. postica*, and Biotic 1 and 2 for *G. rufobrunnea*) are presented. The abiotic model predicting *G. postica* distribution performed fairly well, with an AUC score of 0.819 (Table 2.2). The models predicting *G. postica* host tree distributions had a fair to high predictive power (Appendix A), with test AUC values ranging from 0.72 to 0.87 (Table A1). However, when biotic interactions, in the form of these modelled host tree distributions (Fig. B1−B4, Appendix B) were included in the SDMs of *G. postica*, model predictive power and performance did not improve (Table 2.2).

The known occurrence records of the *G. postica* match well with the current predicted distribution of the species by the abiotic model (Fig. 2.4A), particularly for parts of South Africa, Namibia, Botswana and East Africa where the species has been recorded. Areas that the model predicts to be suitable for the *G. postica* but where the species has not been recorded (i.e. parts of Angola, Zambia, Zimbabwe, Mozambique and Malawi), could represent either model overprediction (i.e. false presences) or undersampled areas where *G. postica* has not yet been recorded. Most of central southern Africa is predicted to be unsuitable for *G. postica*.

When host plant distributions were incorporated into the model as predictors of *G. postica* distribution (Fig. 2.4B & C), the predicted range of the species appears to be more restricted than when they were excluded (Fig. 2.4A). The areas predicted to be suitable for *G. postica* by the biotic models are similar to the predictions made by the abiotic model. However, the biotic models increase the number of false absences (i.e. areas that are predicted to be unsuitable for the species, but where the species and some of its host plants have been recorded) and therefore under-predicts *G. postica* distribution on the west coast of southern Africa.

The models of the distributions of *G. rufobrunnea* host plants performed well (Appendix A), with test AUC values ranging from 0.76 to 0.87 (Table A1). However, both the biotic and abiotic models of *G. rufobrunnea* distribution performed poorly (Table 2.2) and the distribution maps for this species may be unreliable. The poor model performance is also evident from the presence-absence maps generated for these models, which show that the current predicted distribution of *G. rufobrunnea* matches poorly with the known occurrence records of the species (Fig. 2.5). Moreover, the test gain (which is a measure of the goodness of fit) for these models was negative (Table 2.2). There was also a large difference between the test and training AUC scores for these models, which is an indication of the degree of overfitting (Stockwell & Peterson, 2002).

The abiotic model predicted a broader range of suitable conditions for *G. rufobrunnea* than the biotic models (Fig. 2.5), but it performed no better than what a random model would have (test AUC = 0.49). Incorporating the biotic interaction into the model of *G. rufobrunnea* distribution similarly improved all models' predictive powers based on the AUC score, although, this score remained low (Table 2.2).

4.4.2 Gonometa *species future (2070) projected distributions*

The future distributions of the *Gonometa* species were predicted under both RCP scenarios and using all abiotic and biotic models (see Figs. B1−B6 in Appendix B for maps of future host tree distributions used in biotic models). All of the models predicted the distribution of *G. postica* to contract by 2070 (Figs. 2.6–2.8). This is especially evident in the northern areas of the species' southern African range. The models predict that South Africa will remain suitable for *G. postica* by 2070 and that new areas may become suitable for the species, but only if both the moth and its host plants manage to track climate change. Furthermore, the models predict *G. postica*'s distributional range in Kenya to almost disappear. This is more pronounced for biotic (Figs. 2.7 & 2.8) models than for the abiotic model (Fig. 2.6), and is more severe for the IPSL-CM5-LR model simulations (Figs. 2.6–2.8C−D) than the HadGEM2-ES simulations (Figs. 2.6–2.8A−B). Incorporating the biotic interaction into the model of *G. postica* distribution restricts the species' range slightly more than when it is excluded.

All models predicted *G. rufobrunnea* distribution in 2070 (Figs. 2.9–2.11A–D) to be quite similar to the current predicted distribution of the species (Figs. 2.5). Although slight regional changes are evident from the maps, e.g. minimal expansion of the species into South Africa and a slight contraction of the species' East African range, I considered these projections to be unreliable due to the poor performance of the models.

Table 2.2. Model performance for the models of *Gonometa* spp. distributions: Abiotic – models run using climatic predictor variables only; Biotic – models run using climatic variables and host tree distribution as predictors of *Gonometa* spp. distributions. In Biotic 1 probability maps of each host plant distributions were incorporated into the models, whereas in Biotic 2 individual host plant presence-absence maps were used as predictors of moth distribution. For Biotic 3, the presence-absence maps of host plant distributions were combined and incorporated into the models. In Biotic 4, host plant probability maps were summed and used as predictors of moth distribution. The AUC is the area under the curve and is used as a measure of model performance. SD = standard deviation and gain = a likelihood statistic (maximising the probability of *Gonometa* presence in relation to background data) for the test data (i.e. data used to evaluate how well Maxent predicts independent data)

Model	Test AUC	Training AUC	SD AUC	Test gain
G. postica (Abiotic)	0.8187	0.8337	0.0480	0.7398
G. postica (Biotic 1)	0.738	0.8531	0.0659	0.4713
G. postica (Biotic 2)	0.7178	0.8456	0.0741	0.3739
G. postica (Biotic 3)	0.7114	0.8439	0.0725	0.3956
G. postica (Biotic 4)	0.7241	0.8471	0.0678	0.4556
G. rufobrunnea (Abiotic)	0.4934	0.9000	0.1370	-2.0078
G. rufobrunnea (Biotic 1)	0.6455	0.9371	0.1414	-0.6506
G. rufobrunnea (Biotic 2)	0.6374	0.9106	0.1453	-0.8263
G. rufobrunnea (Biotic 3)	0.62	0.9085	0.1449	-1.1679
G. rufobrunnea (Biotic 4)	0.6226	0.9336	0.1441	-1.9269

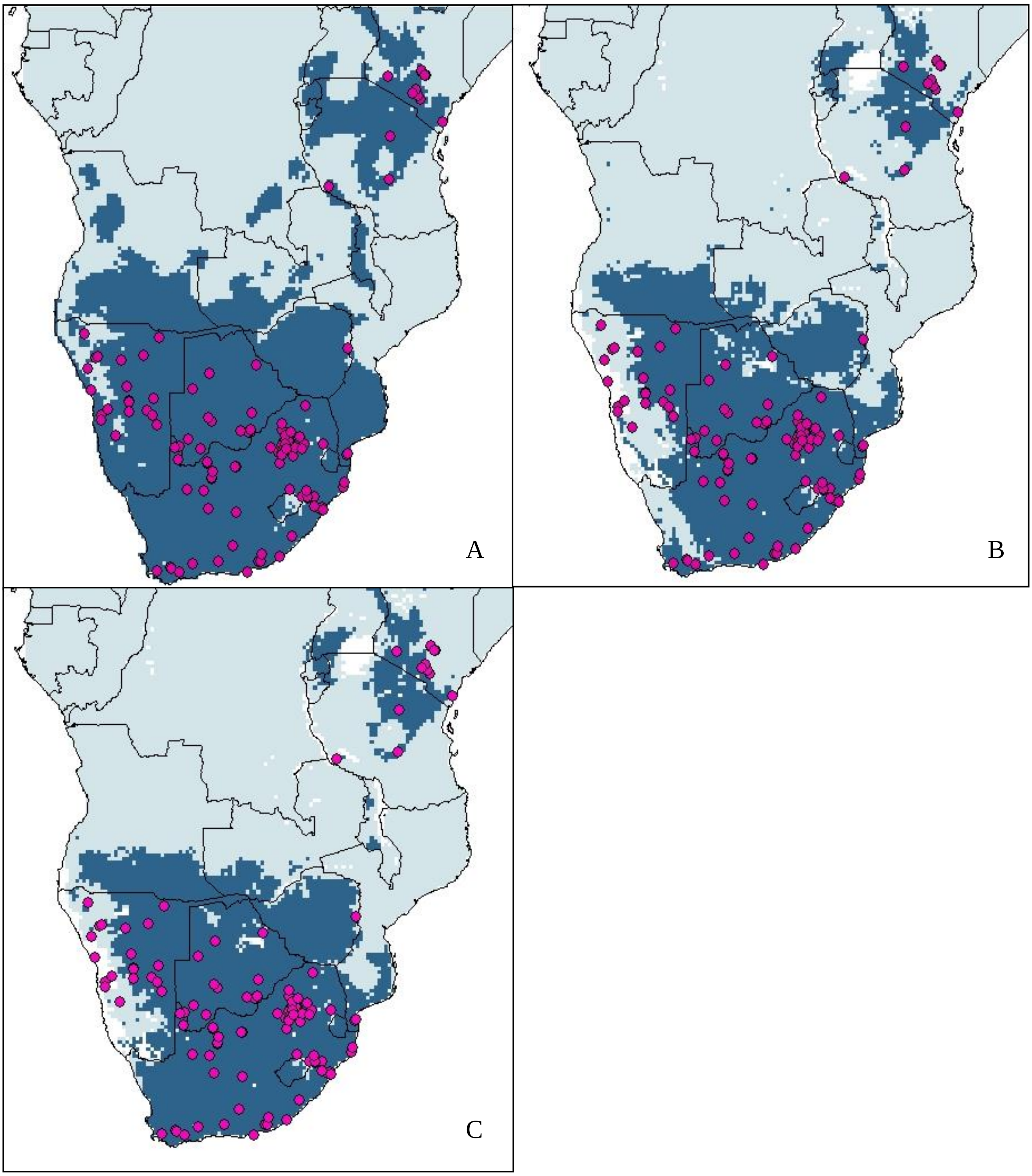


Figure 2.4. Presence-absence maps generated for the current predicted distribution of *Gonometa postica*, where A) only climatic data were use as predictors (Abiotic model), B) the individual probability maps of host plant distributions were used in addition to climate data as predictor variables (Biotic 1), and C) the combined probability maps of host plant distributions were used in conjunction with climate data as predictor variables (Biotic 4). Known occurrence records are illustrated in pink. Dark areas predict *G. postica* presence (suitable areas), and light areas absence (unsuitable areas). Presence-absence maps were generated using the "equate entropy of thresholded and original distributions threshold".

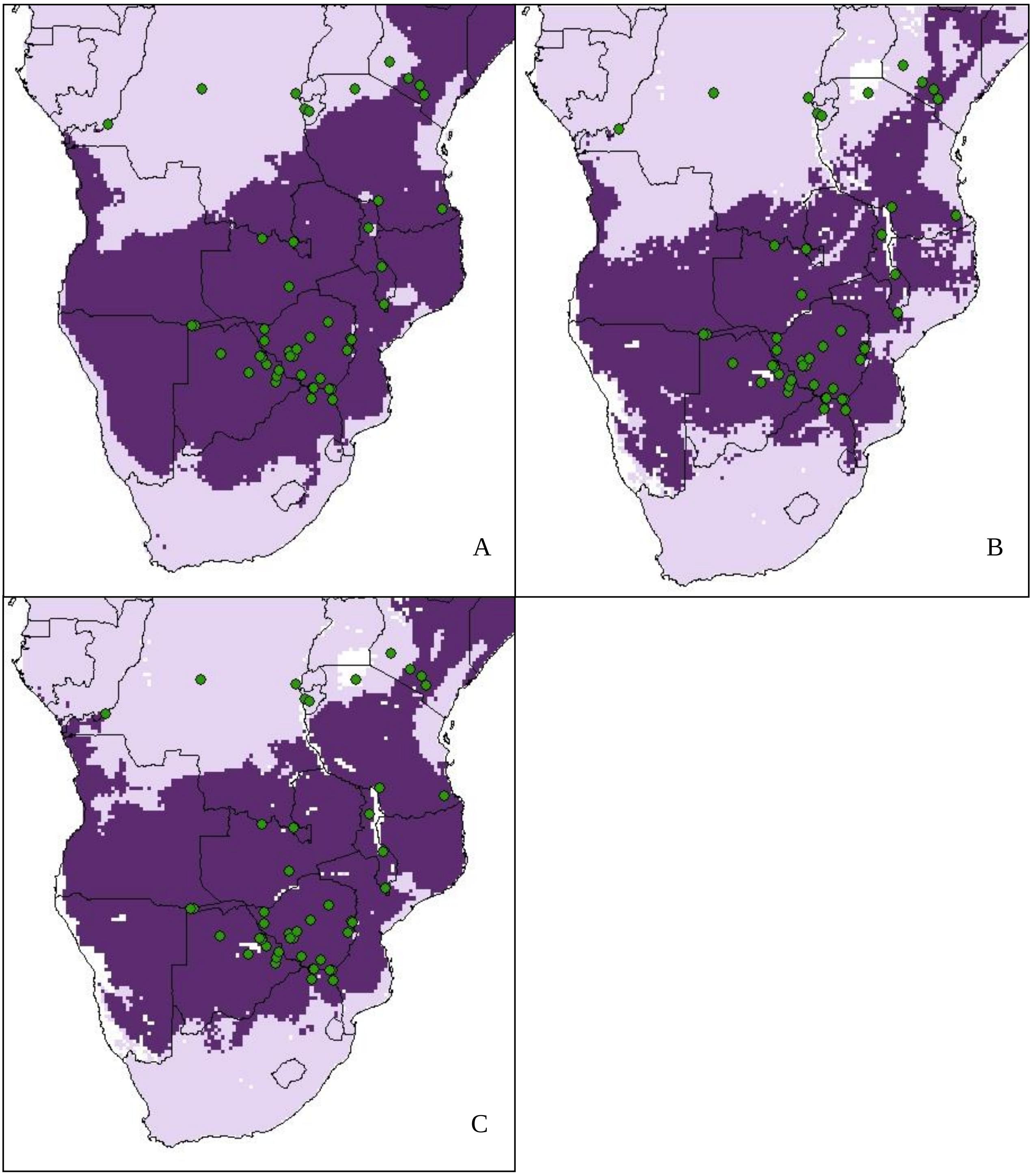


Figure 2.5. Presence-absence maps generated for the current predicted distribution of *Gonometa rufobrunnea* where A) only climatic predictor variables were used (Abiotic model), B) the individual probability maps of host plant distributions were used in conjunction with climate data as predictor variables (Biotic 1), and C) the individual presence-absence maps of host plant distributions were used in addition to climatic data as predictor variables (Biotic 2). Known occurrence records are illustrated in green. Dark areas represent *G. rufobrunnea* presence (suitable areas), and light areas absence (unsuitable areas). Presence-absence maps were generated using the “equate entropy of thresholded and original distributions threshold”.

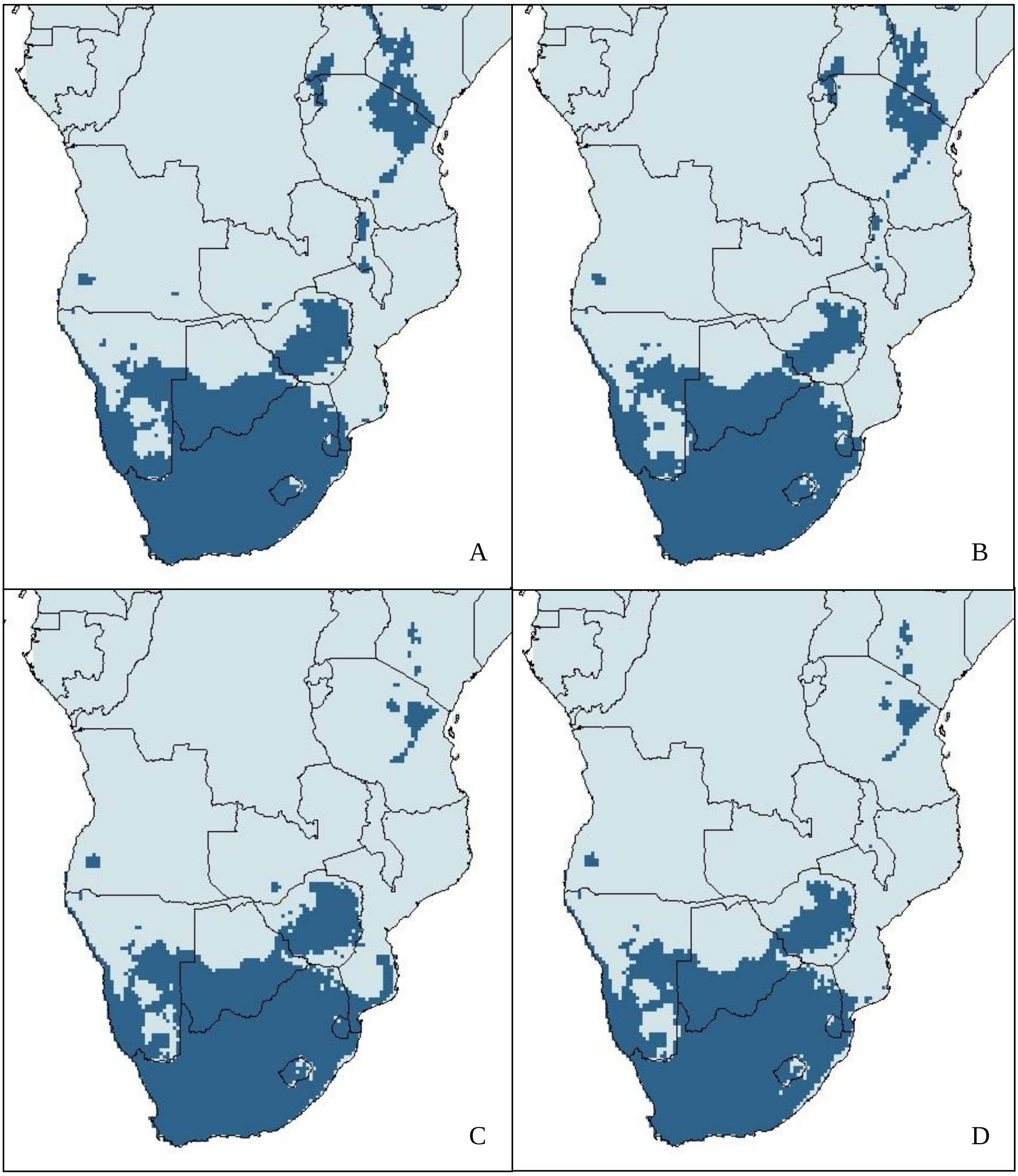


Figure 2.6. Presence-absence map generated for the future (2070) potential distributions of *Gonometa postica*, predicted using only climate data as predictor variables (Abiotic model). Dark areas represent *G. posrica* presence (suitable areas), and light absence (unsuitable areas). The future models were run under two different climate change (RCP) scenarios that were simulated using Earth System and Global Circulation Models: A) RCP 4.5, HadGEM2-ES; B) RCP 6, HadGEM2-ES; C) RCP 4.5, IPSL- CM5A-LR; D) RCP 6, IPSL-CM5A-LR. Known occurrence records are represented in pink for the current predicted *G. postica* distribution. Presence-absence maps were generated using the "equate entropy of thresholded and original distributions threshold".

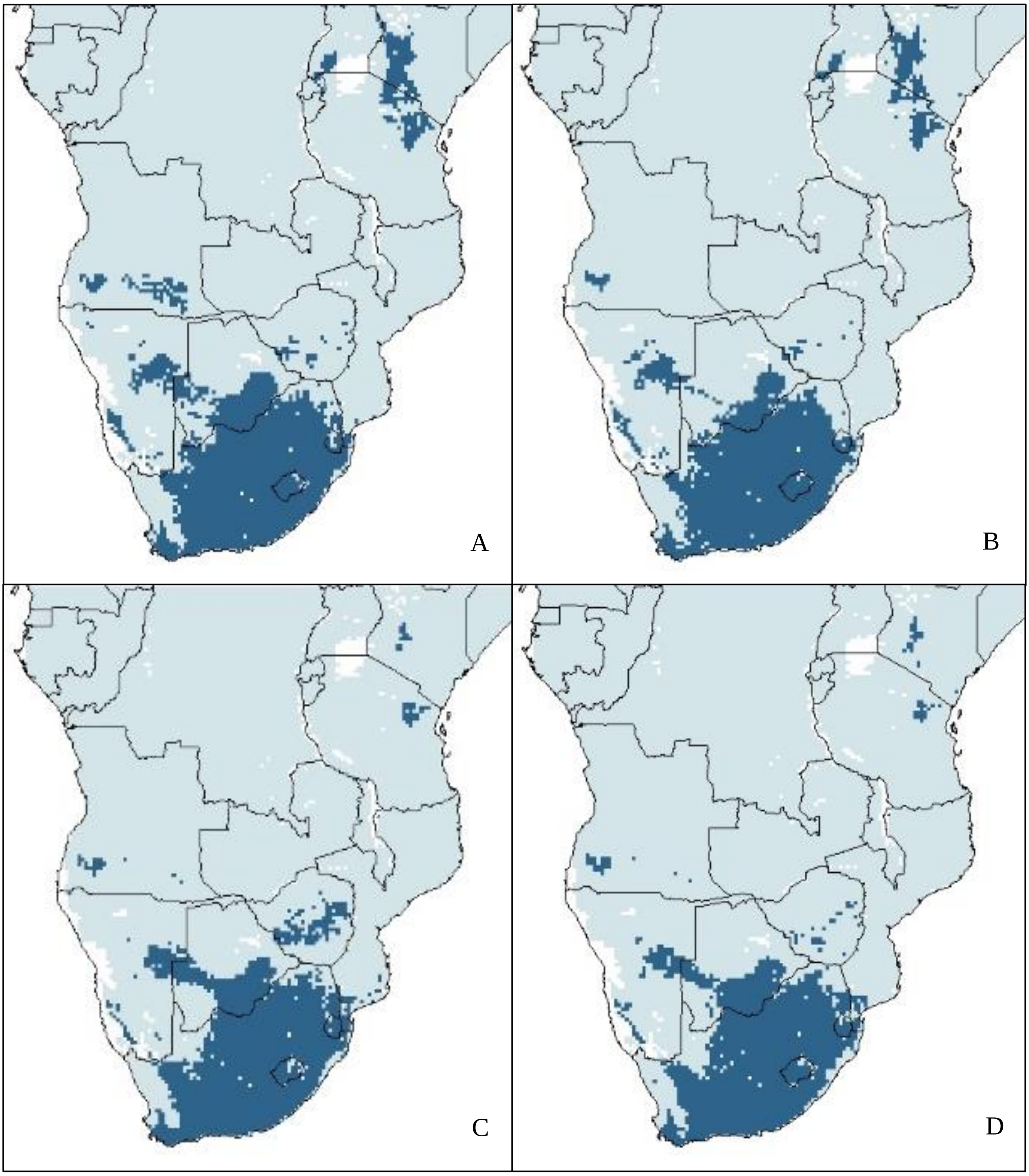


Figure 2.7. Presence-absence maps generated for the future (2070) potential distributions of *Gonometa postica*, predicted using the individual probability maps of host tree distributions in addition to climatic data as predictor variables (Biotic 1). Dark areas represent *G. postica* presence (suitable areas), and light areas absence (unsuitable areas). Future models were run under two different climate change (RCP) scenarios that were simulated using Earth System and Global Circulation Models: A) RCP 4.5, HadGEM2-ES; B) RCP 6, HadGEM2-ES; C) RCP 4.5, IPSL-CM5A-LR; D) RCP 6, IPSL-CM5A-LR. Known occurrence records are illustrated in pink for the current predicted *G. postica* distribution. Presence-absence maps were generated using the "equate entropy of thresholded and original distributions threshold".

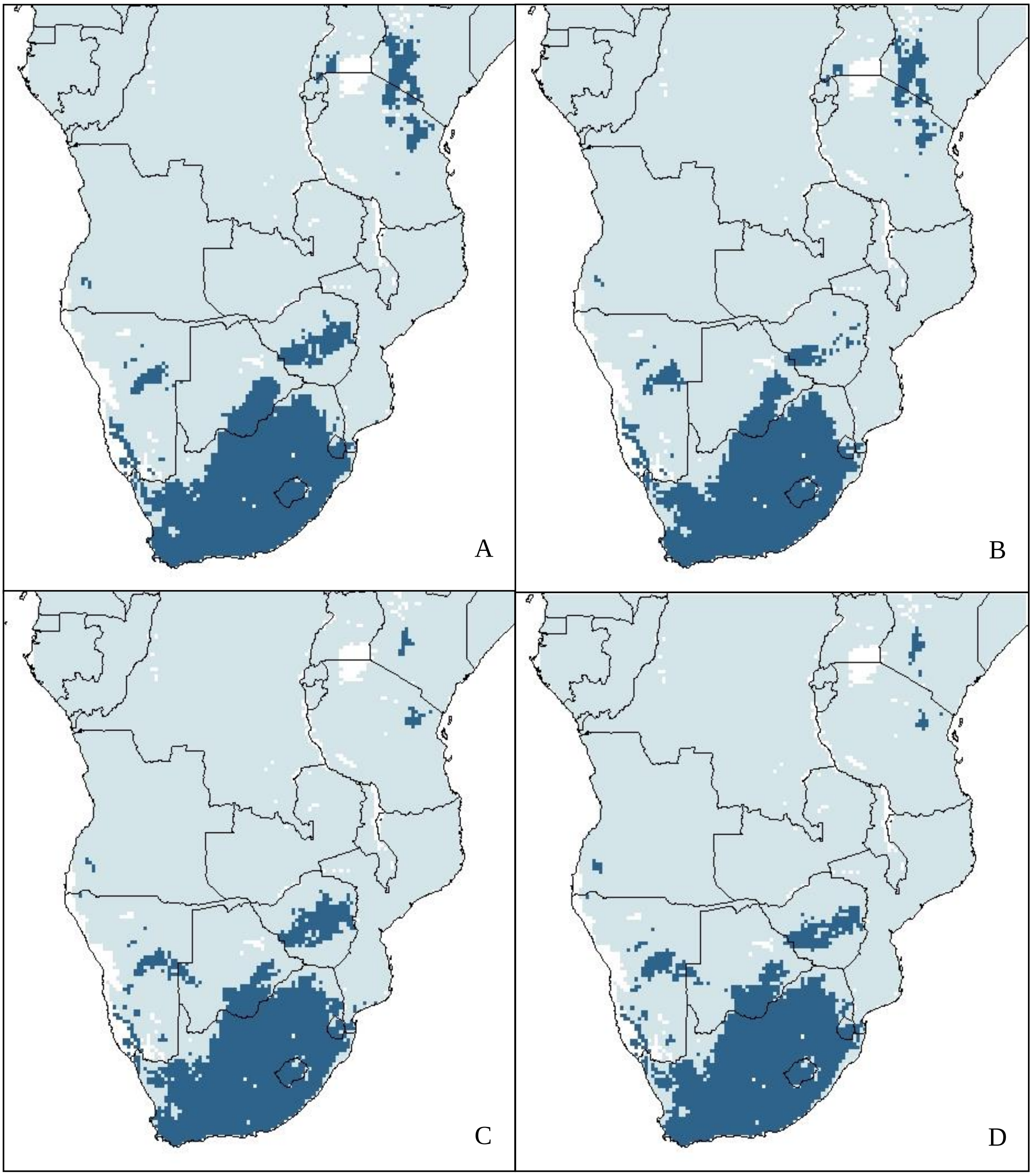


Figure 2.8. Presence-absence map generated for the future (2070) potential distributions of *Gonometa postica*, predicted using climate data in conjunction with the combined host plant probability map as predictor variables (Biotic 4). Dark areas represent *G. postica* presence (suitable areas), and light areas absence (unsuitable areas). Future models were run under two different climate change (RCP) scenarios that were simulated using Earth System and Global Circulation Models: A) RCP 4.5, HadGEM2-ES; B) RCP 6, HadGEM2-ES; C) RCP 4.5, IPSL- CM5A-LR; D) RCP 6, IPSL-CM5A-LR. Known occurrence records are illustrated in pink for the current predicted *G. postica* distribution. Presence-absence maps were generated using the “equate entropy of thresholded and original distributions threshold”.

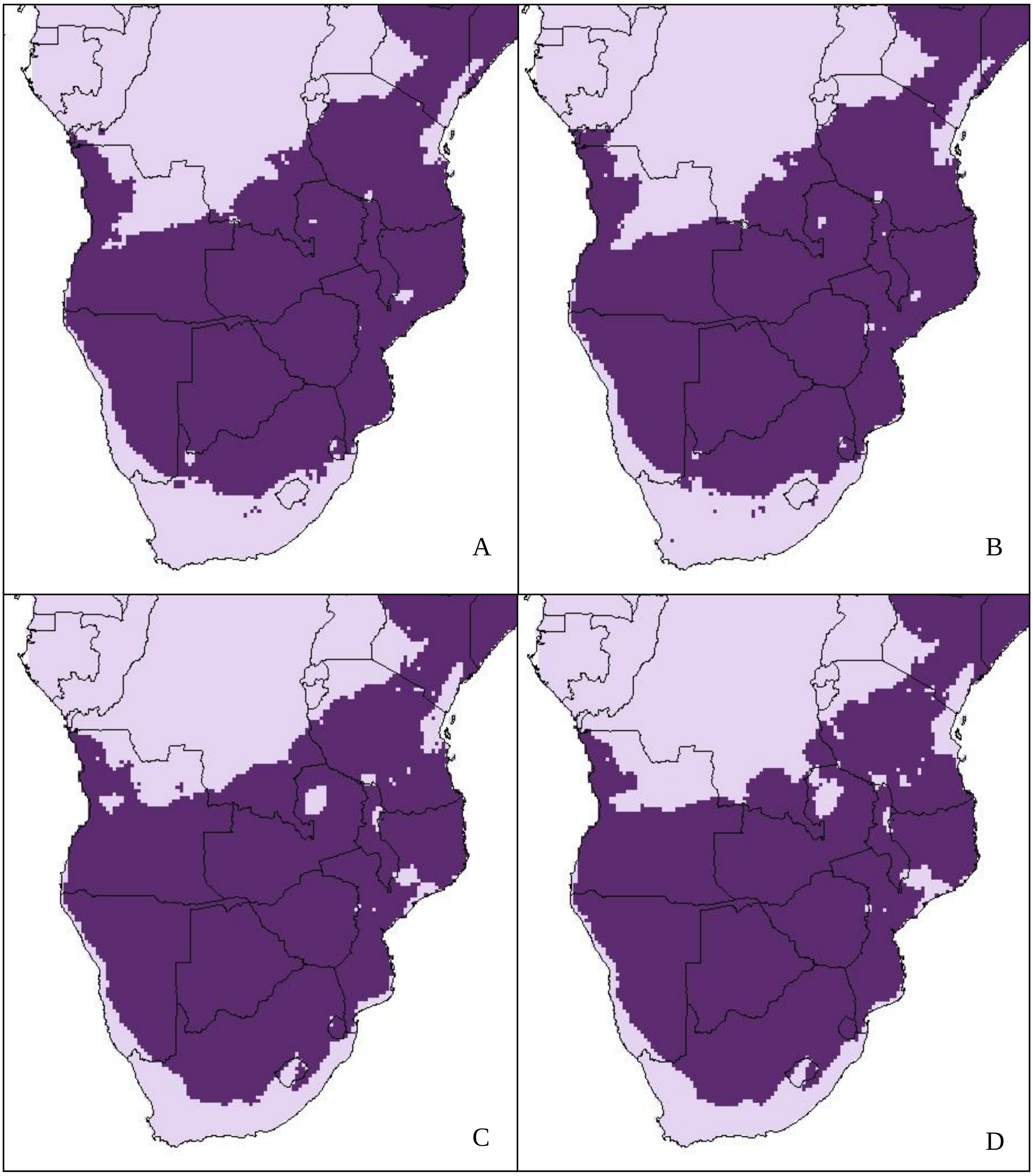


Figure 2.9. Presence-absence maps generated for the future (2070) potential distributions of *Gonometa rufobrunnea*, after using only the climatic data as predictor variables (Abiotic model). Dark areas represent *G. rufobrunnea* presence (suitable areas), and light areas absence (unsuitable areas). Future models were run under two different climate change (RCP) scenarios that were simulated using Earth System and Global Circulation Models: A) RCP 4.5, HadGEM2-ES; B) RCP 6, HadGEM2-ES; C) RCP 4.5, IPSL-CM5A-LR; D) RCP 6, IPSL-CM5A-LR. Known occurrence records are illustrated in green for the current predicted distribution of the species. The maps were generated using the “equate entropy of thresholded and original distributions threshold”.

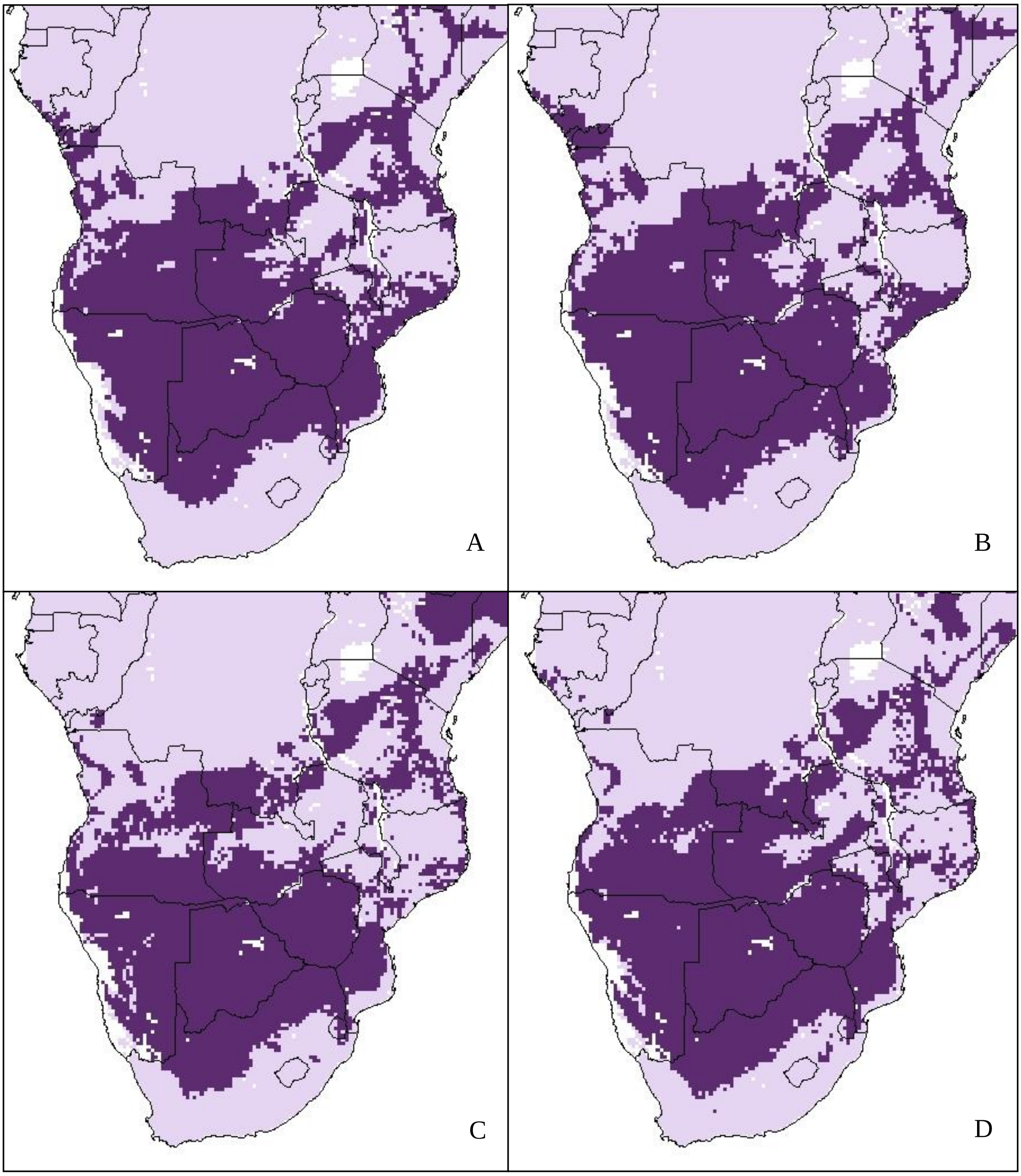


Figure 2.10. Presence-absence map generated for the future (2070) potential distributions of *Gonometa rufobrunnea*, where the probability maps of host tree distributions and the climatic data where used as predictor variables (Biotic 1). Dark areas represent *G. rufobrunnea* presence (suitable areas), and light areas absence (unsuitable areas). Future models were run under two different climate change (RCP) scenarios that were simulated using Earth System and Global Circulation Models: A) RCP 4.5, HadGEM2-ES; B) RCP 6, HadGEM2-ES; C) RCP 4.5, IPSL- CM5A-LR; D) RCP 6, IPSL-CM5A-LR. Known occurrence records are illustrated in green for the current predicted distribution of *G. rufobrunnea*. The presence-absence maps were generated using the "equate entropy of thresholded and original distributions threshold".

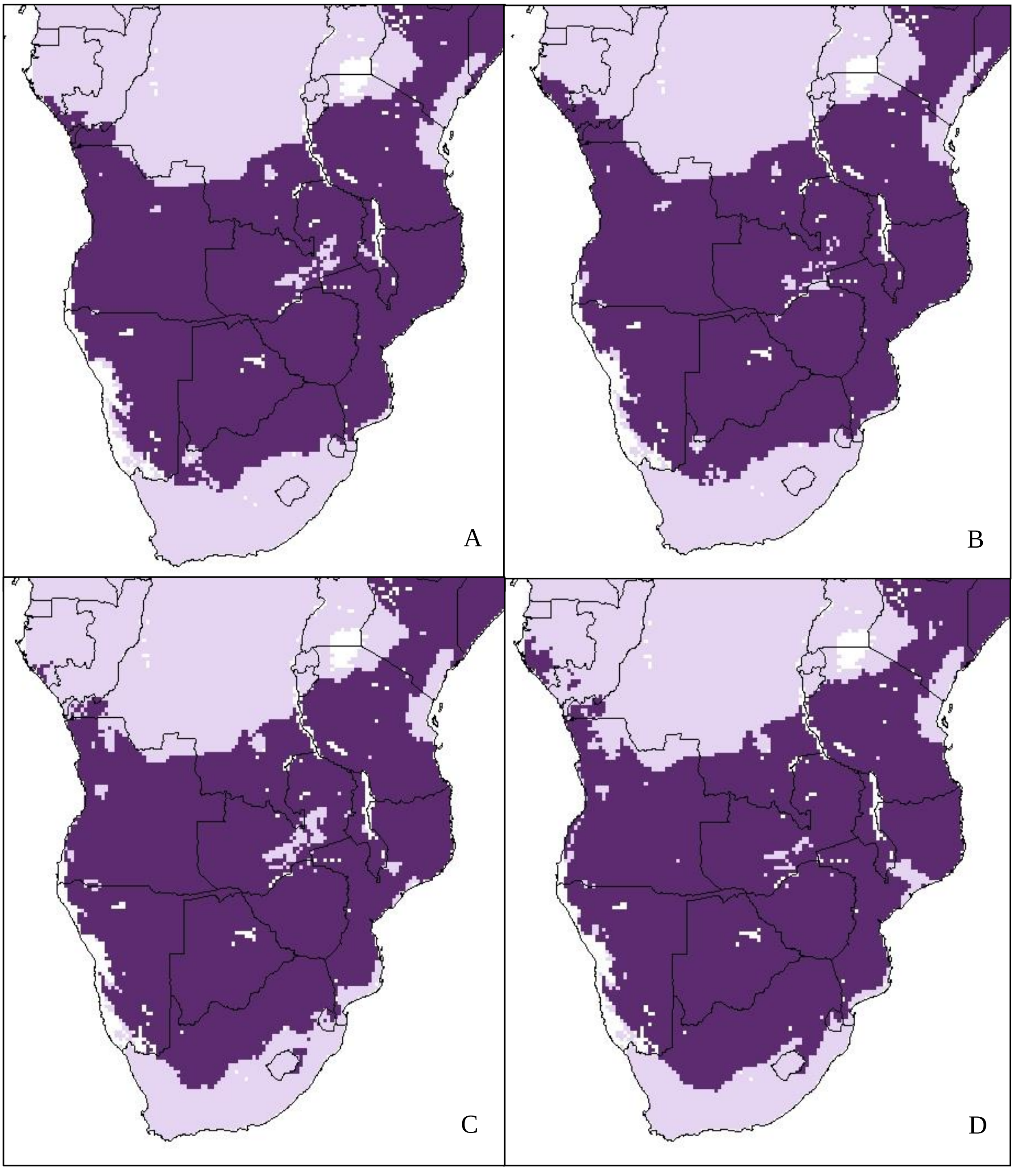


Figure 2.11. Presence-absence map generated for the future (2070) potential distributions of *Gonometa rufobrunnea*, where the presence-absence maps of host tree distributions and the climatic data where used as predictor variables (Biotic 2). Dark represent *G. rufobrunnea* presence (suitable areas), and light areas absence (unsuitable areas). Future models were run under two different climate change (RCP) scenarios that were simulated using Earth System and Global Circulation Models: A) RCP 4.5, HadGEM2-ES; B) RCP 6, HadGEM2-ES; C) RCP 4.5, IPSL-CM5A-LR; D) RCP 6, IPSL- CM5A-LR. Known occurrence records are illustrated in green for the current predicted distribution of the species. The maps were generated using the "equate entropy of thresholded and original distributions threshold".

4.4.3 *Variable contribution and importance*

The variable which contributed most to the Abiotic model of *G. postica* distribution was annual precipitation, with a percentage contribution of 56.4% (Table 2.3). In addition, the jackknife test of variable importance using the training gain revealed that, when considered in isolation, annual precipitation yielded the highest training gain (0.41) compared to the other variables, and therefore contained the most useful information by itself for explaining the model of *G. postica* distribution. This variable also contained the most information that was not included by the other variables, yielding the lowest training gain (0.41) when excluded from the model.

When the probability maps of host plant distributions were incorporated into the model as additional predictors of *G. postica* distribution (Biotic model 1), the percentage contribution of annual precipitation decreased (Table 2.3). *Vachellia erioloba* and *B. africana* became the main contributors to the model. Training gain was lowest when *B. africana* and annual precipitation were excluded from the model (gain = 0.65 and 0.69 respectively), and highest (0.41) when annual precipitation was considered in isolation from the other predictor variables. These variables therefore contained the most unique, useful information not contained by the other variables. Model predictive power was at its lowest (AUC = 0.74) when *B. africana*, *V. erioloba* and annual precipitation were excluded from the model, and for the single predictor models, and at its highest when *V. erioloba* was considered independently from the other predictor variables (AUC = 0.84).

Similarly, for the model which incorporated the combined host plant probability maps as predictor variables (Biotic model 4), the percentage contribution of annual precipitation decreased and host plant distribution became the main contributor of 40.1% (Table 2.3). Annual precipitation contained the most useful information by itself (gain = 0.41) for describing *G. postica* distribution, but host plant distribution contained the most information not included by the other predictor variables in the model (gain = 0.59) and also contributed towards the predictive power of the model. Although annual mean temperature was not the main contributor to this model, the predictive power of the model was lowest when this variable was excluded from the model.

The probability of occurrence of *G. postica* was predicted to increase with annual mean temperature, up until a certain temperature value and thereafter decrease (Figs. C1–C3, Appendix C). Furthermore, the abiotic and biotic models predicted the probability of occurrence of *G. postica* to be highest in areas will low annual precipitation. *Gonometa* *postica* occurrence was predicted to increase with the probability of occurrence of its host tree species (Fig. C2 and Fig. C3).

Precipitation seasonality and host plant distribution contributed highly to the models predicting *G. rufobrunnea* distribution (Table 2.3, Figs. C4−C6, Appendix C). They were also important for defining *G. rufobrunnea* distribution and contributed towards the predictive power of the model (Table 2.3). *Colophospermum mopane* became a main contributor to the model when host tree distributions were incorporated; however, precipitation seasonality remained an important predictor variable. However, because of the poor performance of these models, it is difficult to draw reliable conclusions about the drivers of the species' distribution. This is particularly true for the abiotic model, which performed no better than what a random model would have.

4.5 DISCUSSION

4.5.1 Gonometa *species model performance – biotic versus abiotic variables*

This study compared SDMs with abiotic predictor variables to those with both abiotic and biotic predictor variables. Because the association between *Gonometa* species and their host plants is necessary for the completion of the moths' life cycles (Hartland-Rowe, 1992; Fening *et al.*, 2008; Fening *et al.*, 2010), I expected that host plants play an important role in shaping *Gonometa* distributions, and that incorporating the moth-host plant interaction into the modelling process would improve model predictive power.

Contrary to what was expected, this study found that incorporating the moth-host plant biotic interaction into the model lowered *G. postica* model performance. The opposite was found for the model of *G. rufobrunnea* distribution – incorporating the interaction improved model performance (albeit that the best model's performance was still fairly weak). Biotic interactions have improved model explanatory power at both local (Leathwick & Austin, 2001; Leathwick, 2002; Pellissier *et al.*, 2010) and large (Araújo & Luoto, 2007; Giannini *et al.*, 2013) spatial scales. Indeed, incorporating information on host plant species has been shown to affect the distributions and population dynamics of other Lepidoptera (Araújo & Luoto, 2007; Menéndez *et al.*, 2007; Schweiger *et a*l., 2012; Alalouni *et al.*, 2013). However, inclusion of biotic interactions or other aspects of species' ecologies into the modelling process does not always improve model performance and predictive power (McPherson & Jetz, 2007; Bateman *et al.*, 2012). Observed patterns on one scale may not always be reflected at other scales (Guisan & Thuiller, 2005), so perhaps different results would be obtained if these *Gonometa* species distributions were modelled at a local scale. For example, *Gonometa* distributions may be influenced more by local host tree abundance or quality, which may be mediated by local environmental conditions.

The degree of dietary specialization (or more generally ecological specialization) of a species has been shown to influence model performances (Hernandez *et al*., 2006; Araújo & Luoto, 2007; Preston *et al*., 2008; Giannini *et al*., 2013). Some literature has reported *G. rufobrunnea* to feed only on *C. mopane* (Scholtz & Holm 1985; Hartland-Rowe, 1992); however, it has been reported on other host plants (Kroon, 1999; pers. comm. Richard Peigler). Its northern range stretches considerably further north than *C. mopane*'s northern-most distribution. *Gonometa postica* is considered to be less host specific than *G. rufobrunnea* (pers. comm. Ruan Veldtman). The more dependent one species is on another or on other species, the more likely its distribution is to be shaped by interactions with the species. This may serve as a possible explanation for the slight improvement observed in *G. rufobrunnea* model performance following the inclusion of host plant distributions. Furthermore, modelling species distributions using biotic interactions often requires a greater amount of knowledge on species biology than what is available. (Baselga & Araújo, 2009) For *Gonometa* species, although their life cycles host tree identities have been established, knowledge on their interactions with host trees (i.e. performance on and preferences for certain host plants over others), is limited (e.g. Fening *et al*., 2008; Fening *et al*., 2010). Addressing this research gap could improve predictions of *Gonometa* distributions.

Species' life histories and traits have also been shown to affect model performance (Luoto *et al*., 2005; Pöyry *et al*., 2008; Zurell *et al*., 2009, Hanspach *et al*., 2010; Syphard & Franklin, 2010). As an example, Pöyry *et al*. (2008) found the distributions of butterfly species with greater vagility and longer flight periods to be less accurately predicted by SDMs than butterflies with reduced mobility and flight periods. *Gonometa* species, which are characterised by eruptive, unpredictable population cycles (Veldtman *et al*., 2007), may be influenced by stochasticity within their environments, which could influence model performance (Pöyry *et al*., 2008). For example, personal observations revealed that *G. postica* could be absent from an area following a period of drought in one year, in which it had otherwise been very abundant. Moreover, parasitoids are additional mortality factors acting on *Gonometa* species populations (Hartland-Rowe, 1992; Veldtman *et al*., 2004; Fening *et al*., 2009) and may also play an important role in shaping their distributions, through the effect that they have on *Gonometa* population dynamics and outbreaks. Therefore, biotic models might have improved with the inclusion of parasitoid (and predator) occurrence. Environmental stochasticity in these forms is not well represented by the predictor variables in the models. Moreover, predictor variables do not account for the influence of trait variation within and between host tree species (which could mediate moth oviposition preferences) on *Gonometa* distributions. In some plant-insect systems, plant resources are the dominant factors mediating insect distributions and abundances, whereas in others, presences of natural enemies are more important (Schultz, 1992; McMillin & Wagner, 1998). However, the role of top-down factors (relating to natural enemies) versus bottom-up effects (relating to host plants) in determining species dynamics and distributions remain topic of considerable debate (Hunter & Lechowicz, 1992; McMillin & Wagner, 1998; Jamieson *et al*., 2012). The moth-host plant interactions in my study were not as representative of *Gonometa* distributions as I thought they would be.

Other studies which have used similar methods to model species distributions (i.e. Araújo & Luoto, 2007; Preston *et al*., 2008; Bateman *et al*., 2012) showed that when host plant occurrence was considered in conjunction with climatic variables as predictors of broad-scale species distributions, model performances improved significantly compared to the climate-only models. However, Bateman *et al*. (2012) only found improved model performance when incorporating positive (consumer-resource) interactions into models and not negative (competitive) interactions (which lowered model predictive power slightly). Therefore, biotic model predictive power may be influenced by the interaction types that are incorporated in models, and may be species distributions species-dependent (Schweiger *et al*., 2012; le Roux *et al*., 2012; Eskildsen *et al*., 2013).

4.5.2 *Consequences of climate change for* **Gonometa** *spp. distributions*

Climate projections show that southern and East Africa and its ecosystems will be significantly affected by climate change (Collier *et al*., 2008; Lovett, 2015). Some areas are predicted to become drier and others wetter (Collier *et al*., 2008). Climate change is likely to affect *G. postica* and *G. rufobrunnea* distributions because their periodic outbreaks coincide with seasonal rainfall events (Hartland-Rowe, 1992).

All models predicted a contraction in the range *G. postica*. Additionally, *G. postica*'s range was predicted to shift towards higher latitudes with climate change, which has already been observed in a number of butterfly species (Parmesan *et al*., 1999; Hughes, 2000; Eskildsen *et al*., 2013). Furthermore, *G. postica*'s East African range was predicted to almost disappear by 2070, which could be attributed to the predicted increase in average rainfall in eastern Africa and parts of central Africa (Collier *et al*., 2008). Due to the poor performance

Table 2.3. Variables that were found to be the important (i.e. variables contributing most to the models and which yielded the highest training gain and AUC scores based on the jackknife tests of variable importance) for describing the *Gonometa* spp. distributions. Variables marked with asterisks did not contribute highly to the models based the analysis of variable contribution, but were important predictors of moth distribution based on the jackknife tests of variable importance (training gain and AUC columns). Permutation importance is determined by randomly permuting values of the variable in question among the training points. The gain given in the table starts at 0 during a model run, increasing towards an asymptote and gives the maximum likelihood ratios of average presences to average background points (see Merow *et al*., 2013). Maximizing the gain gives the best models. The training gain without the variable represents the model gain once the variable in question has been removed from the model, whereas the training gain with the variable only, represents the gain of the model when the variable in question is considered in isolation from all the other variables. The AUC (without variable) represents predictive power of the models when the variables in question are excluded from the models, and the AUC (variable only) represents AUC from a model containing only the predictor variable

Species model	Variable	% Contribution to model	Permutation importance	Training gain (without variable)	Training gain (Variable only)	AUC (without variable)	AUC (variable only)
G. postica – (Abiotic)	Annual Mean Temperature	36.79	23.25	0.4771	0.3121	0.7960	0.7800
	Annual Precipitation	56.37	75.75	0.4079	0.4059	0.8013	0.7809
G. postica (Biotic 1)	*Vachellia erioloba*	36.65	0.42	0.7262	0.2161	0.7395	0.8350
	Burkea africana	16.32	28.46	0.6454	0.2251	0.7386	0.6760
	*Senegalia mellifera**	2.96	8.64	0.7018	0.2993	0.7676	0.7071
	*Vachellia tortilis**	1.95	1.87	0.7179	0.2551	0.7433	0.7364
	Annual Mean Temperature*	15.52	9.65	0.7116	0.3430	0.7408	0.7244
	Annual Precipitation*	8.98	30.67	0.6925	0.4081	0.7351	0.7494
G. postica (Biotic 4)	Host plant distribution	40.05	25.95	0.5927	0.3509	0.7416	0.7275
	Annual Mean Temperature	32.88	12.91	0.633	0.343	0.7249	0.7244
	Annual Precipitation*	15.42	48.17	0.6152	0.4081	0.7504	0.7494
G. rufobrunnea (Abiotic)	Annual Precipitation	14.09	20.53	0.7836	0.2860	0.5460	0.3848
	Precipitation Seasonality	79.47	76.87	0.6714	0.7247	0.4989	0.5683
	Precipitation of the Driest Quarter*	6.40	2.57	0.8892	0.4863	0.5036	0.5677
G. rufobrunnea (Biotic 1)	*Colophospermum mopane*	79.77	48.22	1.0133	1.0284	0.6393	0.5950
	Precipitation Seasonality	15.98	44.63	1.1587	0.8763	0.6255	0.6239
G. rufobrunnea (Biotic 2)	Precipitation Seasonality	57.8	84.08	0.838	0.8763	0.6413	0.6239
	Colophospermum mopane	29.9	4.26	0.9747	0.5047	0.6336	0.6502
	Precipitation of Driest Quarter*	11.5	11.00	1.0484	0.5768	0.6433	0.5999
	Annual Precipitation*	0.6	0	1.0813	0.1672	0.6341	0.6414

of the *G. rufobrunnea* models, I consider the SDM predictions of the effect of climate change on the species unreliable.

Climate change could also affect *Gonometa* species distributions indirectly because variations in temperature have been shown to alter insect herbivore population density, development, life cycle duration, host plant exploitation extent, distributions (via novel colonisations or extinctions), voltinism and genetic composition (Hughes, 2000; Bale *et al*., 2002; Braschler & Hill, 2007; Jamieson *et al*., 2012). Temperature changes may also affect insect metabolism and flight activity (Jamieson *et al*., 2012). Rises in temperature, which are expected for northern and southern Africa (Collier *et al*., 2008) could advance lepidopteran flight period and adult emergence (Menéndez, 2007; Jamieson *et al*., 2012) and affect larval development (Fening *et al*., 2010). Furthermore, plants and insects will be affected by climate change either directly, through the modification of insect or plant traits, or indirectly, through changes in organisms with which they interact in other trophic levels (Hunter & Elkinton, 2000; Jamieson *et al*., 2012; Schweiger *et al*., 2012). Therefore, another consequence of climate change is the alteration of species interactions (i.e. *Gonometa*-host plant interactions), which can feed back to species geographical ranges and abundances (Hughes, 2000; Blois *et al*., 2013). Consequently, climate change can narrow and possibly eliminate some of the overlaps, and increase the number of mismatches between *Gonometa* species and their host plants.

Further mismatches between the distributions of the *Gonometa* species and their host plants could occur if climate change shifts the phenologies of these species as demonstrated for species in other studies (Hughes, 2000; Hunter & Elkinton, 2000; Roy & Sparks, 2000; Bale *et al*., 2002; Stefanescu *et al*., 2003; Menéndez, 2007; Forister *et al*., 2010; Jamieson *et al*., 2012). In 1990, late rainfall events resulted in a population crash for *G. rufobrunnea* because moth emergence was triggered by temperature changes, but there was no foliage available on their host trees at this time (Hartland-Rowe, 1992). For many host-specific insect herbivores to successfully complete their life cycles, close synchrony is required with host plant phenology and this becomes more critical as the climatic suitability for insects declines (Bale *et al*., 2002). An additional factor that may have a profound effect on *Gonometa* species distributions into the future is the presence and response of predators, bacteria, viruses and parasites to climate change (Hartland-Rowe, 1992; Jamieson *et al*., 2012). Interactions between these natural enemies and climatic conditions have been shown to affect other lepidopteron population dynamics and distributions into the future (Alalouni *et al*., 2013). They may also lead die-offs in a number of woody plant species as well as changes in the severity and frequency of outbreak species (Logan *et al*., 2003). Such mortality factors are active throughout the life cycle of *Gonometa* and vary through space, time and in intensity depending on *Gonometa* population densities (Hartland-Rowe, 1992; Veldtman *et al*., 2004).

Changes in species responses have implications for *Gonometa* species and the silk harvesting industry which depends on them, because the current distributions of the moths are dependent on the current distribution of their host trees. Mismatches between the two could lead to population crashes (Menéndez, 2007). Species may also shift to novel host plants. However, *G. postica* do show preferences for certain host tree species over others (see Fening *et al*., 2008). Moreover, although *G. postica* has been observed on different host tree species, my observations in the field showed that *V. erioloba* was the only tree where the moth was found, even though different host tree species were present. Such regional preferences would make shifts to novel host tree species difficult.

4.5.3 *Drivers of current* **Gonometa** *species distributions*

Gonometa postica occurs in more temperate regions than *G. rufobrunnea*, and appears to be limited by annual precipitation. In contrast, precipitation seasonality was the most important predictor for the distribution of *G. rufobrunnea*. These abiotic variables were important predictors of *Gonometa* distribution irrespective of inclusion of exclusion of host plant data. These results are in broad agreement with studies showing that *Gonometa* species are dependent on both temperature and precipitation cues for outbreak initiation and emergence from cocoons (Hartland-Rowe, 1992, Delport, 2006). This suggests that climate could exert a role (Pearson & Dawson, 2003) in shaping *Gonometa* species distributions broad scales; although, the effect of host tree distributions cannot be ignored (Araújo & Luoto, 2007; Schweiger *et al*., 2012).

The abiotic models for both *G. postica* and *G. rufobrunnea* predicted a broader set of suitable conditions for these moths than the biotic models, which contrast with Bateman *et al*. (2012) who found that incorporating consumer-resource interactions into models increased the area of suitable habitat for species. This suggests that host plant distributions limit the current predicted and future potential distributions of *Gonometa,* likely due to the association between *Gonometa* species and their host plants for development and survival (Veldtman *et al*., 2007; Fening *et al*., 2008; Fening *et al*., 2010); i.e. models may predict climatic suitability for the moths in certain regions, but if their host plants are absent from those regions, they would be unable persist there. *Gonometa* species range limits may also be attributed to multiple species interactions (Case *et al*., 2005; Schweiger *et al*., 2012) occurring within these systems. For example, competition, predation or facilitation among species and individuals, can inflate or restrict species ranges (Pulliam, 2000). Furthermore, host plants may mediate insect oviposition preference and therefore drive insect distributions via differences in host plant traits or qualities (McMillin & Wagner, 1998). For example, *G. postica* has demonstrated a preference for certain host tree species over others in East Africa (see Fening *et al*., 2008).

4.6 CONCLUSION

Results obtained in this study contrast with previous studies which have found improved SDM performance by incorporating consumer-resource interactions into models predicting large-scale species distributions. However, predictions made by the biotic models contrasted to predictions from the abiotic models for the current and especially future predicted range of the species concerned. My results supported the idea that climate governs the large scale distributions of species; however, the importance of the moth-host plant interactions in shaping *Gonometa* species distributions should not be ignored. Literature suggests that the effects of biotic and abiotic factors in shaping species distributions are dependent on the species involved, and vary with species' biology, ecology and traits (Luoto *et al*., 2005; Hernandez *et al*., 2006; Pöyry *et al*., 2008; Zurell *et al*., 2009; Syphard & Franklin, 2010; Schweiger *et al*., 2012); however, for *Gonometa* species distributions, further studies are required to investigate the contribution and importance of these factors.

Furthermore, to predict the effects of climate change on species distributions, there is a need to better understand species interactions (Gilman *et al*., 2010; Bateman *et al*., 2012) and how each partner in the interaction will respond to climate change (Jamieson *et al*., 2012). Both partners in an interaction have the potential to respond individually to climate change. Therefore, by including biotic interactions into the modelling process, I assume my predictions of the impact of climate change on species distributions are more realistic as opposed to climate-only models (Araújo & Luoto, 2007; Gilman *et al.*, 2010). This is especially true for *Gonometa* species, which are dependent on their host trees for survival. Future work is needed to strengthen the ecological theory behind *Gonometa*-host plant interactions (such as possible regional specialization on dominant host plant species), which may improve my predictions of *Gonometa* distributions. The importance of host-plant interactions shaping *Gonometa* species distributions relative other factors such as *Gonometa*-parasioid interactions and natural enemy responses to climate change also needs to be assessed.

CHAPTER 3

Empty *G. postica* cocoons act as ecosystem engineered structures for arboreal ants on *Vachellia erioloba*

Licences and permits

Licence to use *Vachellia erioloba*: NCU 4640714
To authorise cut, remove and damage or destroy: a) indigenous trees in natural forests, and/or b) protected trees, or the acquisition or disposal in any manner of such trees or their products.
Valid: 1 July 2014 - 31 December 2016

Permits for the collection and transport of biological material: a) FAUNA 424/2/2014, b) FAUNA 1736/2014, c) FAUNA 1737/2014
Fauna research
Valid: a) 5 May 2014 - 5 May 2017
Valid: b) 9 December 2014 - 9 December 2017
Valid: c) 9 December 2014 – 9 June 2015

5.1 INTRODUCTION

The numerous biotic interactions and abiotic conditions that a species experiences may determine its niche, and as a result, its habitat choice (Jeffries & Lawton 1984; Palmer, 2003). Biotic interactions that strongly affect species habitat choice may include competition for limiting resources (food and space), predation and parasitism. In some cases, species habitat choice may also be mediated by positive (i.e. mutualistic) interactions with other species (Kaminski *et al.*, 2010) or by organisms that alter resource flow by changing the physical states of biotic or abiotic materials through ecosystem engineering (Jones *et al.*, 1994; Jones *et al.*, 1997; Dangerfield *et al.*, 1998).

Ecosystem engineers alter their environments in such a way that it benefits themselves or, either directly or indirectly, other organisms (Jones *et al.*, 1994; Jones *et al.*, 1997; Breitburg *et al.*, 2010). They create, modify or maintain habitats, increasing local patchiness and, usually, alter population dynamics and support different species than to environments from which ecosystem engineers are absent (Dangerfield *et al.*, 1998; Jones *et al.*, 1997; Gutiérrez *et al.*, 2003). Consequently, ecosystem engineers promote habitat heterogeneity and can affect patterns and processes at the individual, population or community level (Badano & Marquet, 2008).

Autogenic ecosystem engineers are those which alter the environment via their own physical structures (e.g. plants, mussels or biofilm-producing microbes) (Jones *et al.*, 1997; Dangerfield *et al.*, 1998; Jones *et al.*, 2006). In contrast, allogenic ecosystem engineers transform materials from one physical state into another (Dangerfield *et al.*, 1998; Jones *et al.*, 2006; Kawai & Tokeshi, 2006). These include, for example, soil cast-creating earthworms, tree-felling elephants and dam-building beavers (Jones *et al.*, 1997; Gutiérrez *et al.*, 2003; Jones *et al.*, 2006; Breitburg *et al.*, 2010). Ecosystem engineers have long been recognised for the positive impact that they have on species assemblages, although their impacts on species can also be negative (Lill & Marquis, 2003). The effects of ecosystem engineers on other organisms may either be strong or weak and are dependent on the engineer involved (Jones *et al.*, 1997).

In arboreal systems, there are many examples of herbivorous invertebrate ecosystem engineers, which include leaf-tying, leaf-rolling and leaf-folding caterpillars, leaf miners and wood-boring beetles (Martinsen *et al.*, 2000; Fukui, 2001; Fournier *et al.*, 2003; Lill & Marquis, 2003; Kagata & Ohgushi, 2004; Lill & Marquis, 2004; Lima *et al.*, 2013). They create shelters within the trees that are frequently utilized by other taxa (including Diptera, Coleoptera, Lepidoptera, Hymenoptera, Hemiptera and Orthoptera) as refuges against negative bottom-up or top-down effects (Fukui, 2001). These shelters influence the abundance, survival and distribution of other species, and can therefore shape local patterns of species diversity.

Arboreal ants are known to utilise a wide variety of plant structures as potential nesting sites (Beattie & Hughes 2002). For example, some species use specialized thorn domatia (Campbell *et al*., 2013b), and other domatia in the form of hollow stems, leaf pouches and petioles (Heil & McKey, 2003) and cavities that occur naturally (Dejean *et al*., 2012). Studies on the ant utilization of thorn domatia have found that individual trees can be occupied by either single or multiple ant species (Davidson & McKey, 1993; Young *et al*., 1997; Palmer, *et al*., 2000; Raine *et al*., 2004; Palmer *et al*., 2010; Stanton & Palmer, 2011; Palmer & Brody, 2013). There is also evidence for ants using structures created by other organisms, such as leaf shelters, as nesting sites (Nakamura & Ohgushi, 2003).

In this study, ants and other invertebrates were observed using the cocoons of the economically important silk moth species, *Gonometa postica* Walker 1855, on the myrmecophilic tree *Vachellia erioloba* (one of *G. postica*'s main hosts in South Africa) (Hartland-Rowe, 1992; Campbell *et al*., 2013a). The larvae of these moths forage on the foliage of the trees for approximately two months before spinning cocoons (Hartland-Rowe, 1992), which allows for direct interactions between *G. postica* and the arboreal ants. The association between *G. postica* caterpillars and ant species on *V. erioloba* is antagonistic (Campbell *et al*., 2013a). The ant species, which inhabit thorn domatia on *V. erioloba*, display aggressive behaviour towards foraging *G. postica* larvae, where they remove the larvae from trees. However, empty *G. postica* cocoons may serve as ant sheltering and nesting sites (similar to thorn domatia), potentially providing a buffer for ants and other invertebrates against environmental extremes and natural enemies, creating a unique and protected environment. The cocoons, like other engineered structures, likely create a new abiotic state which is different from the unmodified abiotic conditions (Jones *et al*., 2006) and may impact the overall complexity associated with the tree (Lill & Marquis, 2003). *Gonometa postica* may therefore be considered an autogenic (Jouquet *et al*., 2006) ecosystem engineer because it constructs structures that are utilised by ants and other invertebrates within the trees (Martinsen *et al*., 2000; Lill & Marquis, 2003; Jones *et al*., 2006; Lima *et al*., 2013).

This chapter examines the ecological significance of *G. postica* as an ecosystem engineer for acacia ants and other invertebrates. No previous research has examined the secondary utilization of invertebrate-created biogenic structures by ants, making this a novel study. I hypothesise that ants are selecting cocoons as nesting sites based on aspects of cocoon morphology (i.e. size), similar to what has been observed for ant nest or domatia selection (Thomas, 2002; Campbell *et al*., 2013b). *Gonometa postica* is sexually dimorphic, with cocoons varying in shape, length and width (Veldtman *et al*., 2002), and therefore providing varying amounts of space for ants. Furthermore, different hole types (i.e. small parasite holes; and/or large moth emergence holes) are present in vacant *G. postica* cocoons. The selection of cocoons by ants may be based on these hole types, because acacia ants (Campbell *et al*., 2013b) and other invertebrates (Fincke, 1999; Kagata & Ohgushi, 2004) have been observed selecting nesting sites based on differences in entrance hole sizes. I also hypothesise that ants may be selecting cocoons based on the number of holes present within the cocoons and on the positions of the cocoons in the trees which may influence the microclimate within the cocoons.

Lastly, *V. erioloba* trees host aggregations of honeydew-producing scale insects, which produce liquid food rewards for ants in return for protection against natural enemies (Heil & McKey, 2003; Gibbs & Cunningham, 2009; Pringle *et al*., 2011). While scale insects may be widespread, they do not occur on every tree. This further complicates the *G. postica*-ant interaction because these food sources are one of the main mediators of ant distributions and behaviour towards herbivores within trees (McKey, 1984; Gibbs & Cunningham, 2009). Moreover, the ant species may be co-existing with one another and with other invertebrates within *G. postica* cocoons, which parallels ant species co-existence observed within domatia on *V. erioloba* (Campbell *et al*., 2013a; Campbell *et al*., 2013b). To my knowledge, no other studies have reported ant species co-occupancy within individual myrmecophyte domatia or other arboreal nests. Therefore, I hypothesise that the ants' associations with scale insects and the presence of other invertebrates within the cocoons could influence ant nest site or cocoon selection.

5.2 AIMS

This chapter aims to examine the potential ecosystem engineering effect created by *G. postica* cocoons for ants associated with the *G. postica* host plant, *V. erioloba.* More specifically, I will:

- examine whether ant presence and abundance within cocoons is mediated by cocoon characteristics
- examine if ant presence and abundance within cocoons is affected by the presence of scale insects on *V. erioloba* and the incidence of ants tending the scale insects.
- examine whether all, or only some of the *V. erioloba*-associated ant species using the

cocoons are using cocoons as potential nesting sites.

- examine patterns of ant species occurrence and co-occurrence in the cocoons and trees

5.3 METHODS

5.3.1 *Study site and study species*

Fieldwork was conducted on Oppiknoppi Guest Farm, near Hotazel in the Northern Cape Province, South Africa (26°39’48”S, 22°43’04”E). The farm lies in the Kalahari, which is an arid component of the savanna biome (Knobel & Bredenkamp, 1999). The area receives about 400 mm rainfall p.a. and is characterised by deep, sandy soils. Dominant trees at the site include *V. erioloba*, *Senegalia mellifera* and *Boscia albitrunca*, which are sparsely scattered between a variety of grass and shrub species.

Vachellia erioloba is of economic value for commercial firewood and is threatened by illegal, uncontrolled harvesting (Seymour & Milton, 2003). It is also of ecological importance because it promotes habitat heterogeneity, thereby increasing species richness though provisioning of habitats for a variety of flora and fauna (Dean *et al*. 1999). In the Kalahari, *V. erioloba* is the main the host tree of *G. postica*. Several ant species are known to inhabit the domatia of *V. erioloba* trees (Campbell *et al*, 2013b). Furthermore, ants have been observed inhabiting *G. postica* cocoons on *V. erioloba* in this area (personal observation) and in areas of Namibia (personal observation: H. Campbell).

5.3.2 *Field work: sampling*

Gonometa postica cocoons were sampled on *V. erioloba* trees as this was the only plant species on which cocoons were found in any abundance. None of the cocoons were occupied by *G. postica* and may have originated from the last outbreak of the species in this area (i.e. in the year 2012 or 2013). Sampling was conducted in December 2014 and January 2015 over a period of 16 days in the mornings between 5:30 and 12:00, or in the late afternoons. One hundred and ninty seven trees were sampled within six transects that were set up at distances greater than 20 m from farm roads to eliminate edge effects. For each transect, a starting point (focal tree) was randomly selected. The two nearest neighbouring trees of the focal tree were then selected. Thereafter, the next focal tree (located within a 90° angle at least 10 m away from the previous focal tree) was randomly selected and its two nearest neighbours identified again. This selection procedure was repeated by walking along the length of the transect (Catana, 1963). Only trees ranging in height from 1.5 m to 5 m were sampled because no cocoons were found on trees less than 1.5 m in height and it would have been difficult to count and sample all cocoons on trees with heights exceeding 5 m.

Tree trunks and branches were examined for the presence of ants, which were identified to morphospecies (Table 3.1). The percentage cover (0%, <1%, 0-10%, 10-15%, 15-20%, 20-25%, 25-30%, 30-40% and > 40% of branches) of scale insects per tree was visually estimated. If scale insects were present, whether ant-tending of scale insects was happening was recorded, and in the cases where tending was present, the morphospecies of the tending ant species was recorded. Finally, the presence or absence of swollen thorn domatia (see Campbell *et al*., 2013b) was recorded for each tree.

Table 3.1. Ant morphospecies identified on *Vachellia erioloba* trees and within *Gonometa postica* cocoons

Genus/Morphospecies used
Crematogaster sp. 1 (Myrmicinae)
Crematogaster sp. 2 (Myrmicinae)
Cataulacus sp. (Myrmicinae)
Camponotus sp. (Formidinae)
Nesomyrmex sp. (Formidinae)

Every *G. postica* cocoon that could be reached by hand or by the use of a 1 m pole was collected from the tree and placed into its own, labelled plastic container. For each collected cocoon, the host tree identity, aspect (i.e. whether the cocoon was collected from the north or south sides of the host tree) and the time of collection were recorded. Cocoons which contained one or more small holes (mean diameter = 2.68 mm) were categorized as parasitized; cocoons containing a larger hole (mean diameter = 6.72 mm) towards the apex of the cocoon (with a characteristic three-fold split) were considered to be emerged (i.e. cocoons from which fully-developed moths had emerged) and those which contained both large holes towards the apex and small holes were considered as emerged with secondary holes. Two additional cocoon metrics, namely cocoon distance to tree trunk and the number of holes (irrespective of hole type) present within collected cocoons were also recorded for the cocoons from approximately one third of the trees (hereafter referred to as the reduced dataset).

Sampled cocoons were frozen to kill invertebrate occupants. The length and width of each collected cocoon was measured and recorded using a digital calliper, and the cocoons were cut open and the number, morphospecies and life stage of ants (adults, juveniles and eggs) within each cocoon recorded. Presence and identity of other invertebrates within the cocoons were also recorded. Ants sampled from the cocoons were stored in 75 % ethanol and their identities were confirmed by an expert (Dr. H. Campbell) at the University of Pretoria.

5.3.3 *Statistical analyses*

Ant abundance data were both zero-inflated and overdispersed. Data were therefore analysed using hurdle models, which involve two separate analyses (Rose *et al*., 2006). One analysis assesses the positive (count) data with a linear model, whereas the other compares zeros to non-zeros with a binary model. Furthermore, because several cocoons were collected from each tree, cocoons from the same tree could not be considered independent. Therefore, hurdle models were run as generalized linear mixed effects models (hurdle GLMMs), with tree identity as a random effect (see Bolker *et al*., 2008). A truncated negative binomial distribution with a log-link function was fit to all analyses on count data to correct for overdispersion (Rose *et al*., 2006), and the binary models were fitted using a binomial distribution and the logit-link function.

To ascertain if ants were selecting *G. postica* cocoons based on cocoon characteristics, a mixed effects hurdle was run to test whether overall ant abundances and ant presence-absence within cocoons were influenced by cocoon aspect, cocoon length and width, and cocoon hole type. Also included as predictors were presence-absence of other invertebrates within the cocoons, and time of day that the cocoons were sampled (as a quadratic) as these may have affected ant abundance or occurrence of ant species.

In a second analysis, the reduced dataset (which included only the subset of cocoons for which number of holes and the distance of the cocoon from the tree trunks were recorded) was used. In this analysis, the cocoon characteristics listed in the previous paragraph and the two additional cocoon descriptors were used as predictors of ant abundance and ant presence-absence.

A third mixed effects hurdle model was analysed to understand whether ant abundance and occurrence within cocoons could be predicted as a function of the presence of scale insects on the trees, the presence of ants tending scale insects and the time of day that the observations were made. No cocoon characteristics were included as predictors for this analysis.

Lastly, GLMMs were used to examine whether presence-absence of each ant morphospecies was influenced by cocoon characteristics (i.e. using cocoon length, cocoon width, cocoon aspect and hole type present in the cocoon as predictors of morphospecies presence-absence). I also wanted to see if morphospecies occurrence within cocoons was influenced by the presence of other invertebrates within the cocoons, while controlling for the time of day that the cocoons were sampled.

For each component of the hurdle models (count data and binary analyses), and for the GLMM, model selection was done by forward stepwise regressions, which selected the best models based on model AIC scores. All models were tested against null models. Data were analysed in R v.3.0.2 (R Core Team, 2013) using the glmmADMB, Rcmdr and CAR packages.

5.4 RESULTS

5.4.1 *Do cocoon characteristics influence ant abundance and presence-absence?*

5.4.1.1 The effect of cocoon characteristics on ant abundance and occurrence

A total of 702 emerged or parasitized *G. postica* cocoons were sampled from 124 *V. erioloba* trees. Cocoon width, hole type and the presence of other invertebrates within the cocoons were significantly related to ant abundance (Table 3.2). Ant abundance was greatest in cocoons that only had one small exit hole (Fig. 3.1A), and in cocoons from which other invertebrates were absent (Fig. 3.1B). Moreover, larger cocoons contained significantly more ants (Fig. 3.1C). The occurrence of ants in cocoons was also influenced by hole type and the presence of other invertebrates (Table 3.2). Ants were also more likely to be present in cocoons with a single small hole than in cocoons with emergence and/or secondary holes (Fig. 3.1D) and in cocoons from which other invertebrates were absent (Fig. 3.1E). Although cocoon aspect, time of day sampled and cocoon length were included in the minimal adequate model, they were not significant predictors of ant presence-absence.

The final model for the reduced dataset yielded similar results to the large dataset (Table D1, Appendix D). However, none of the additional cocoon descriptors from the reduced dataset were included in the minimal adequate model. Therefore, this model is not considered further.

5.4.1.2 Is ant abundance and presence related to the presence of scale insects and tending incidence of scale insects?

The presence of scale insects on *V. erioloba* trees, the presence of ants tending scale insects and the time of day that the cocoons were sampled were either not included in the minimal adequate model or had no significant effect on ant abundance in *G. postica* cocoons (Table 3.3). However, scale insect presence did have an effect on ant presence in the cocoons; ants were most likely to be present in *G. postica* cocoons on trees that hosted scale insects (Table 3.3, Fig. 3.2).

Table 3.2. Results from the minimum adequate mixed effect hurdle models testing the effects of cocoon characteristics on (A) ant abundance (n = 339 cocoons, n = 95 trees, $p < 0.05$) and (B) presence-absence (n = 702 cocoons, n = 124 trees, $p < 0.05$) in *Gonometa postica* cocoons on *Vachellia erioloba.* Abbreviations: P = cocoons containing one or more small parasite holes; E = emerged cocoons and ES = emerged cocoons with secondary holes; Pr = other invertebrates present and Ab = other invertebrates absent; N = north aspect and S = south aspect

A. Fixed effects	Level	Estimate	SE	z value	p-value
(Intercept)	-	2.562	0.335	7.650	< **0.001**
Width	-	0.090	0.017	5.330	< **0.001**
Hole type	P > ES > E	-	-	-	**0.018**
Time of day	-	-0.016	0.009	-1.680	0.094
Other invertebrates	Pr > Ab	-	-	-	< **0.001**
Random effect	SD	Variance			
(1|Tree)	0.451	0.203			

B. Fixed effects	Level	Estimate	SE	z value	p-value
(Intercept)	-	-1.189	0.691	-1.720	0.085
Hole type	P > E = ES	-	-	-	< **0.001**
Time of day	-	-0.026	0.016	-1.590	0.111
Other invertebrates	P > A	-	-	-	< **0.001**
Length	-	0.033	0.018	1.880	0.061
Aspect	N = S	-	-	-	0.086
Random effect	SD	Variance			
(1|Tree)	0.830	0.688			

5.4.2 *Do cocoon characteristics influence ant morphospecies occurrence or co-occurrence in* **G. postica** *cocoons?*

5.4.2.1 *Morphospecies occurrence within trees and* G. postica *cocoons*

The same ant genera that were recorded on the branches of the trees were present in *G. postica* cocoons. However, the two *Crematogaster* species, were found to co-occupy some cocoons. *Cataulacus* sp. and *Crematogaster* sp. 1 were the most abundant ant species per cocoon on average (Fig. 3.3A); however, the highest overall abundance was observed when the *Crematogaster* species co-occupied cocoons. *Crematogaster* sp. 1 had the highest number of juveniles within cocoons (Fig. 3.3B), while only one juvenile was present for *Crematogaster* sp. 2 and none for *Nesomyrmex angulatus*.

Trees were most commonly occupied by a single ant species, with few trees co-occupied by two species (Table 3.4). Only 4 trees were co-occupied by three different ant species. *Crematogaster* sp. 1 was dominant, occupying cocoons on 87 trees in total and 66 of these trees exclusively (i.e. without any other ant species) (Table 3.4). *Nesomyrmex angulatus* and *Camponotus* sp. were rarely recorded in cocoons on the trees and may not be specifically associated with *V. erioloba*. About half of the cocoons sampled (i.e. 52%) on the trees were unoccupied by ants (Table 3.4); however, 24% of these unoccupied ant cocoons were occupied by other invertebrates (i.e. spiders, caterpillars and/or beetles). *Crematogaster* sp. 1 was the most commonly encountered ant species within *G. postica* cocoons, occurring in 270 of the sampled cocoons. The remaining morphospecies groups all occurred in less than 25 of the sampled cocoons (Table 3.4). Cocoons were most commonly occupied by single ant species. Shared occupancy was rare, with co-occurrence being observed for the two *Crematogaster* morphospecies within 25 of the sampled cocoons. *Crematogaster* sp. 1 was the only ant species found to co-occur in cocoons with other invertebrates regularly.

5.4.2.2 Do cocoon characteristics affect morphospecies abundance and occurrence within cocoons?

Due to most morphospecies being only infrequently recorded, analyses testing the effect of cocoon characteristics on morphospecies presence-absence were only conducted for *Crematogaster* sp. 1 and *Crematogaster* sp. 2. I was also able to test the effect of cocoon characteristics on the abundance of *Crematogaster* sp. 1 because of its dominance within the cocoons (Table D2, Appendix D). The analyses yielded similar results to the analysis on all ant species, which was expected, because the *Crematogaster* species were dominant in the cocoons. Cocoons containing small holes only housed significantly more *Crematogaster* sp. 1 individuals than cocoons containing only emergence holes (Table D2). Furthermore, this species was significantly more abundant in cocoons from which other organisms were absent. The abundance of *Crematogaster* sp. 1 was also affected significantly by cocoon width, where abundance was greater within wider cocoons as opposed to narrower cocoons.

Cocoon size, i.e. cocoon length, and cocoon length and width, were also significant in predicting the occurrence of *Crematogaster* sp. 1 and *Crematogaster* sp. 2 respectively (Table 3.5). A decrease in cocoon length marked a significant increase in the probability of occurrence of *Crematogaster* sp. 1 in cocoons. However, the opposite was true for *Crematogaster* sp. 2. Furthermore, the probability of occurrence of *Crematogaster* sp. 2 decreased as cocoon widths increased. No significant differences were observed between morphospecies presence-absence and the other cocoon characteristics for the dataset, possibly due to the small sample size.

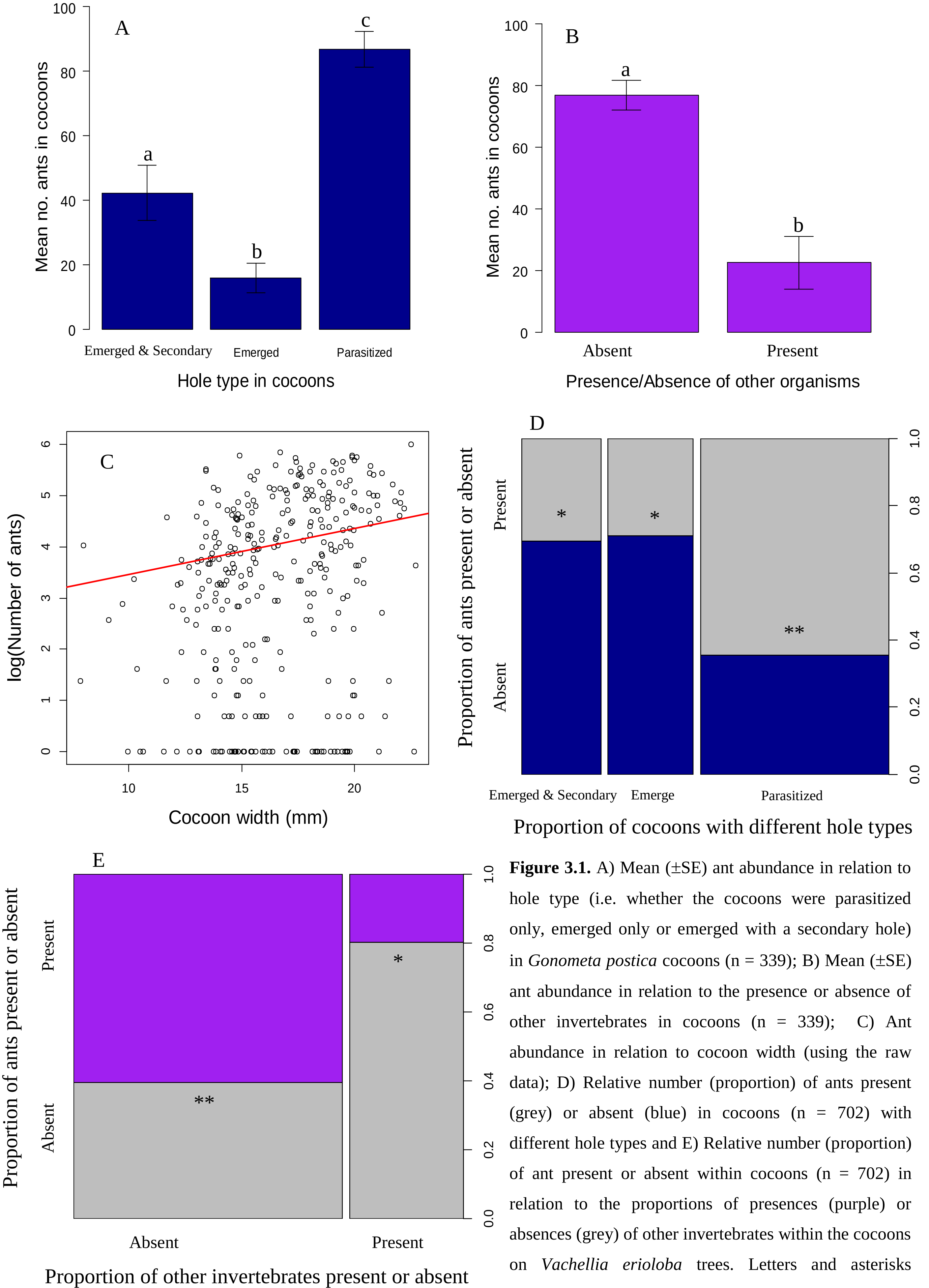


Figure 3.1. A) Mean (±SE) ant abundance in relation to hole type (i.e. whether the cocoons were parasitized only, emerged only or emerged with a secondary hole) in *Gonometa postica* cocoons (n = 339); B) Mean (±SE) ant abundance in relation to the presence or absence of other invertebrates in cocoons (n = 339); C) Ant abundance in relation to cocoon width (using the raw data); D) Relative number (proportion) of ants present (grey) or absent (blue) in cocoons (n = 702) with different hole types and E) Relative number (proportion) of ant present or absent within cocoons (n = 702) in relation to the proportions of presences (purple) or absences (grey) of other invertebrates within the cocoons on *Vachellia erioloba* trees. Letters and asterisks indicate significant differences.

Table 3.3. Results from the minimum adequate hurdle models, testing the effects of presence or absence of scale insects, the incidence of ants tending scale insects on the trees and time of day that sampling took place on (A) total ant abundance (n = 99 trees, p = 0.033) and (B) ant presence-absence (n = 195 trees, p < 0.05) within all *Gonometa postica* cocoons per tree. Abbreviations: Pr = present and Ab = absent

A. Variable	Level	Estimate	SE	z value	p-value
(Intercept)	-	5.391	0.163	33.010	< **0.001**
Ants tending scales	Pr = Ab	-	-	-	0.052
Time of day	-	-0.013	0.009	-1.420	0.154

B. Variable	Level	Estimate	SE	z value	p-value
(Intercept)	-	-1.334	0.362	-3.680	< **0.001**
Scale insects	Pr > Ab	-	-	-	< **0.001**
Time of day	-	0.038	0.020	1.940	0.052

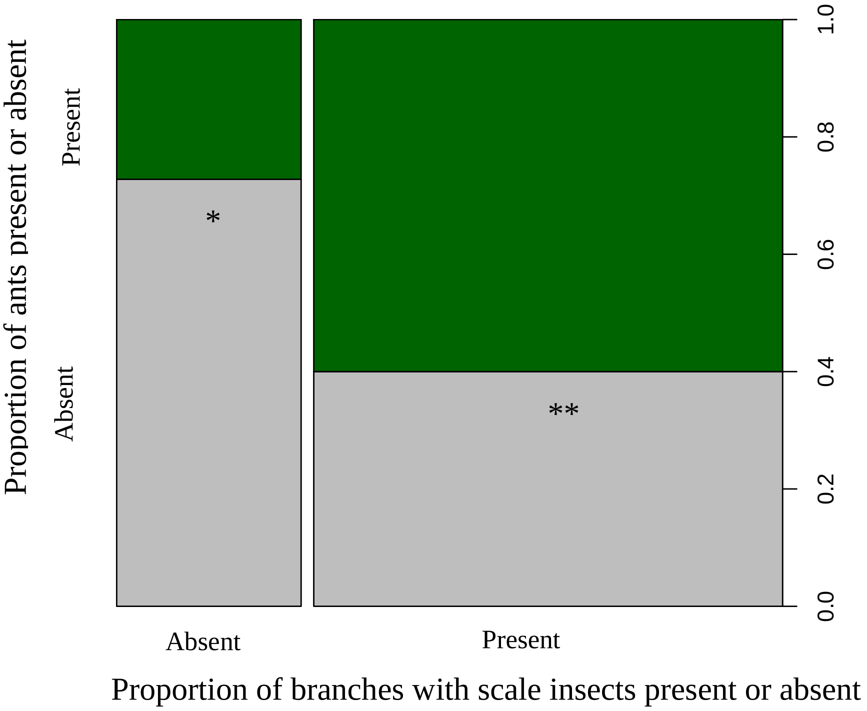


Figure 3.2. Relative number (proportion) of ants present (green) or absent (grey) in *Gonometa postica* cocoons in relation to the proportion of scale insect present or absent on branches of *Vachellia erioloba* trees (n = 195). Asterisks indicate significant differences.

5.5 DISCUSSION

5.5.1 *Do cocoon characteristics influence ant abundance and presence-absence?*

My results demonstrated a novel ecological role of *G. postica*, with ants and other invertebrates using *G. postica* cocoons as nesting sites and for shelter. Arboreal ants are territorially dominant and often occur on myrmecophytes such as *V. erioloba* (Campbell *et* *al.*, 2013a), which they protect from herbivores in exchange for food rewards or nesting sites in the form of thorn domatia (Vasconcelos, 1991; Young *et al*., 1997; Heil & McKey, 2003; Dejean *et al*., 2008; Palmer *et al*., 2008; Stanton & Palmer, 2011; Campbell *et al*., 2013a). No thorn domatia were recorded for the *V. erioloba* individuals sampled in my study; however, ants appeared to secondarily occupy and house their brood within vacant *G. postica* cocoons. This was surprising because arboreal ants have been observed to behave aggressively towards *G. postica* on *V. erioloba* by removing larvae from the trees (Campbell *et al*., 2013a). In this study area, it is unknown if the associated ant species display a similar aggressive behaviour towards *G. postica* larvae; however, some of these ant species are most likely the same ant species that have been reported to behave aggressively towards *G. postica* larvae on *V. erioloba* in Namibia. Harvesting larvae and cocoons from these trees could negatively impact ant species that utilise *G. postica* cocoons as nesting sites because cocoon presence is dependent on larvae survival. Arboreal ants were abundant in *G. postica* cocoons and the manner in which the cocoons were used is comparable to that involving myrmecophyte thorn domatia (Fonseca, 1999; Campbell *et al*., 2013b).

Ant species are known to nest exclusively in individual myrmecophytes, while in some cases they share myrmecophytes (Young *et al*., 1997; Palmer, 2004; Palmer *et al*., 2008; Campbell *et al*., 2013a; Campbell *et al*., 2013b). Space may be a limiting factor in such systems because an increase in colony size likely brings about stronger competition within and between ant species (Fonseca, 1999). However, in this study nest site availability is unlikely to have been a limiting factor because some cocoons were unoccupied by ants or other invertebrates. Low ant occupancy of available nesting sites has been reported from other studies (Sagata *et al*., 2010), possibly due to ants migrating between nests as a form of temperature control (Jones & Oldroyd, 2007). Ants may also need to migrate into larger nests or thorn domatia following an increase in colony sizes (Partridge *et al*., 1997; Palmer, 2003). Therefore, although some cocoons were unoccupied by ants, they may have been previously occupied by them.

All of the trees sampled in this study contained empty *G. postica* cocoons; however, some trees contained very few cocoons. In these cases, and in trees from which cocoons are absent, ants are probably more vulnerable to the elements because of their sensitivity to temperature and humidity (Porter, 1988; Roces & Núñez, 1989 Hood & Tschinkel, 1990), particularly in stressful environments. Nest sites provide more favourable microclimates for ants and their brood (Blüthgen & Feldhaar, 2010). Therefore, when the usual nesting structures are absent or limited within trees, it would be more beneficial for ants to occupy alternative plant structures rather than to nest in the open. Examples of these alternative structures include naturally occurring tree cavities within tree bark, twigs or rotting wood and aerial soil that has accumulated in branch forks (Tanaka *et al.*, 2010; Dejean *et al.*, 2012). Ants may also construct their own nests in the absence of suitable nesting sites (Dejean *et al.*, 2010). In this study no alternative nesting sites were observed, so it is unclear where the ants shelter in the absence of *G. postica* cocoons.

When selecting nesting sites, ant colonies can make choices based on the quality and value of each nesting site relative to others (Mallon *et al.*, 2001; Pratt *et al.*, 2002; Thomas, 2002). Of the occupied *G. postica* cocoons, ant abundance and occurrence were highest and more probable in cocoons that contained parasite holes only (which are the smallest hole types within the cocoons). Similarly, Pratt and Pierce (1991) found that the cavity-dwelling ant species, *Leptothorax curvispinosus*, displayed a preference for cavities that had small entrance hole sizes. A preference for cocoons with smaller holes could be because these cocoons show greater thermal buffering and higher humidity levels (Jones & Oldroyd, 2007).

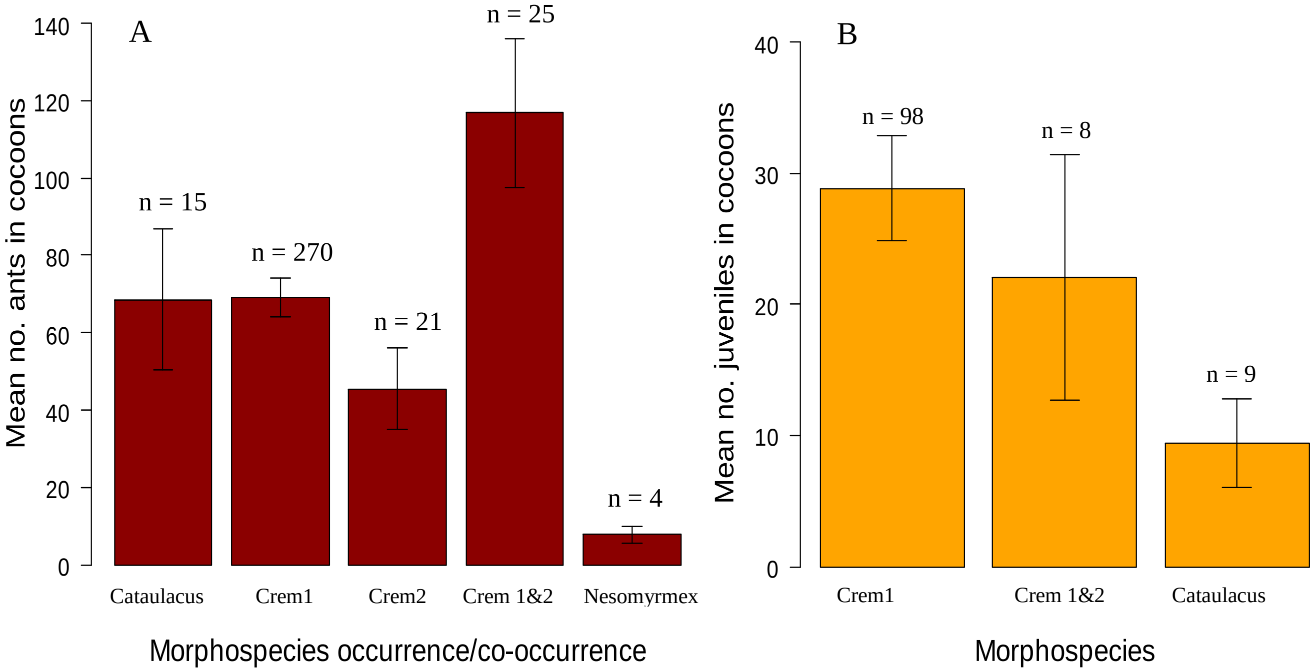


Figure 3.3. A) Mean ± (SE) abundance of ant morphospecies occurring or co-occurring morphospecies within *Gonometa postica* cocoons (n = 336 cocoons). B) Mean ± (SE) abundance of juvenile ants for *Crematogaster* sp. 1 from n = 46 trees, *Crematogaster* spp. co-occupants from n = 6 trees and *Cataulacus* sp. from n = 7 trees. The number of cocoons (n = *x*) from which each morphospecies and juveniles morphospecies were recorded is indicated above the bars. Morphospecies are indicated on the x axes: Crem1 = *Crematogaster* sp. 1, Crem2 = *Crematogaster* sp. 2 and Crem1&2. = *Crematogaster* sp. 1 & 2 co-occupants.

Desiccation (Hood & Tschinkel, 1990) and heat (Porter, 1988; Roces & Núñez, 1989) are important stresses for ant species. Ant preference for cocoons with smaller hole types may also be explained in terms of the possible refuges that they provide to the ant workers and their brood from competitors and predators (Blüthgen & Feldhaar, 2010), because nest entrance hole size influences the ability of ants to defend their nests (Palmer, 2003; Powell, 2009). The lower ant abundance from cocoons with emergence holes and/or secondary holes compared to parasitized-only cocoons also suggests possible niche differentiation related to variation in nest site cavity sizes (see Powell *et al*., 2011). Optimal entrance hole sizes differ between cavity-dwelling species (Powell *et al*., 2011) and this can promote species co-existence between arboreal invertebrates in trees. It is possible that by selecting *G. postica* cocoons based on cocoon characteristics, ant species and other invertebrates could co-exist on individual *V. erioloba* trees, comparable to nest site selection observed for other ant communities (Fonseca, 1999; Sagata *et al*., 2010; Campbell *et al*., 2013b).

Ants (Federle *et al*., 2001; Palmer *et al*., 2002) and other invertebrates (Shenoy & Borges, 2008) have also been shown to create and modify holes within domatia to exclude dominant ant species from taking over; however, I was unable to determine if ants displayed a similar behaviour when selecting and occupying *G. postica* cocoons. It seems unlikely that the holes present in the parasitized-only cocoons in this study were created by the ants because these holes match the description and sizes of holes created by *Gonometa* parasitoids (Veldtman *et al*., 2004; Veldtman, 2005). However, the secondary holes in the emerged cocoons are most likely created by ants because if *G. postica* larvae in the cocoons were parasitized, then they would not be able to emerge (i.e. having emergence holes together with parasite holes is not possible).

Higher ant abundance was found in larger cocoons, in agreement with studies of domatia where domatia size constrains colony size (Thomas, 2002; Shenoy & Borges, 2010; Campbell *et al*., 2013b). Thus, it appears that larger nests allow ants to support more individuals and brood. Moreover, utilization of the biggest domatia or nesting sites could allow for greater investment of ant species into their brood because large domatia can accommodate more brood than smaller domatia (Campbell *et al*., 2013b). My results showed that the *Crematogaster* species appeared select *G. postica* cocoons based on larger cocoon width and length respectively. This is comparable to studies in which different ant species selected nests basted on nest sizes (Fonseca, 1999; Campbell *et al*., 2013b). *Cataulacus* sp. and the *Crematogaster* spp. were the largest bodied ants in my study. Large ants tend to avoid the smallest domatia because increases in their in their colony sizes can result in space becoming limited very quickly, and polydomy would have to occur. Polydomy requires more energy expenditure (e.g. travelling between nests, communication, resource sharing and defence) and also increases colony exposure to natural enemies (Fonseca, 1999). Therefore, it would be more beneficial for larger ant species to occupy larger cocoons.

5.5.2 *Scale insect presence*

Ant presence in cocoons on trees was significantly positively affected by the presence of scale insects. Honey-dew-producing homopterans play an important role in structuring arboreal ant communities (Blüthgen *et al*., 2004). They represent a key resource for the ants (Davidson *et al*. 2003) and therefore have the ability to influence ant habitat choice. *Crematogaster* species were the most commonly encountered species tending the scale insects on the trees in this study, which mirrors observations from other studies (Campbell *et al*., 2013a). This is further supported by other studies which have found that one or two dominant ant species usually monopolize honeydew sources, making their co-occurrence with other scale insect-tending ant species rare (Blüthgen & Fiedler 2002; Blüthgen *et al*., 2004). Scale insects were absent from some of the sampled trees in this study; however, scale insect presence was related to ant presence in *G. postica* cocoons. Moreover, when scale insects were present on the trees, ants were observed tending them. These results suggest that scale insect presence on trees may be an important factor for nest site selection of arboreal ants.

5.5.3 *Ant morphospecies occurrence and co-occurrence in trees and cocoons*

Trees and cocoons were predominantly occupied by one ant species, but in some cases simultaneously by different ant species. *Crematogaster* sp. 1 was the most commonly encountered species in the sampled cocoons. This is not unusual because *Crematogaster* species frequently dominate the trees in which they nest and are very territorial in colony defence (Dejean *et al*., 2010; Stanton & Palmer 2011). Moreover, *Crematogaster* species often have large colonies which are polydomous (Dejean *et al*., 2008; Palmer *et al*., 2010) and competitively exclude or displace other ant species in arboreal systems (Fonseca, 1999; Palmer *et al*., 2000).

Shared occupancy of cocoons was observed for *Crematogaster* sp. 1 and *Crematogaster* sp. 2, and in this combination contained the highest brood abundance in the cocoons compared to the other morphospecies groups; although, I do not know if the brood belonged to both species. Finding more than one founding queen in individual domatia is very rare

Table 3.4. Number of trees (n = 124) on which each ant morphospecies occurred in total, and number of trees that were exclusively occupied by the ant species (i.e. other ant species were not recorded on the tree). Cocoons occupied: total number of cocoons (n = 702) occupied by each ant morphospecies. Shared occupancy of trees: the number of trees in which cocoons occupied by the ant species and cocoons occupied exclusively by invertebrates were recorded; and 2) cocoons: the number of cocoons that were co-occupied by the ant morphospecies and other invertebrates. Ants occupied a total of 336 cocoons, co-occupied 25 cocoons with other ant species and co-occupied 41 cocoons with other invertebrates. A total of n = 194 cocoons contained neither ants nor other invertebrates

Morphospecies	Trees occupied		Cocoons occupied	Shared occupancy	
	Total	Exclusively	Total	Trees	Cocoons
Crematogaster sp. 1 (Myrmicinae)	87	66	270	26	37
Crematogaster sp. 2 (Myrmicinae)	11	4	21	3	0
Crematogaster sp. 1 & *Crematogaster* sp. 2 co-occupants	14	1	25	5	3
Cataulacus sp. (Myrmicinae)	9	1	15	5	1
Camponotus sp. (Formidinae)	1	1	1	0	0
Nesomyrmex sp. (Formidinae)	1	0	4	0	0

Table 3.5. Results from the minimum adequate mixed effect models testing the effects of cocoon characteristics on the presence-absence of A) *Crematogaster* sp. 1 and B) *Crematogaster* sp. 2 (in n = 336 cocoons). Abbreviations: P = cocoons containing one or more small parasite holes; E = emerged cocoons and ES = emerged cocoons with secondary holes

A. Presence-Absence *Crematogaster* sp. 1 ($p < 0.05$) ~	*Fixed effects*	Level	Estimate	SE	z-value	p-value
	(Intercept)	-	6.64	1.893	3.51	< **0.001**
	Length	-	-0.085	0.04	-2.13	**0.033**
	Random effect	SD	Variance			
	(1|Tree)	3.124	9.757			

B. Presence-Absence *Crematogaster* sp. 2 ($p < 0.05$) ~	*Fixed effects*	Level	Estimate	SE	z-value	p-value
	(Intercept)	-	13.452	4.324	3.11	**0.002**
	Width	-	-0.712	0.346	-2.06	**0.040**
	Hole type	P = ES = E	-	-	-	0.281
	Length	-	0.263	0.188	1.4	0.163
	Random effect	SD	Variance			
	(1|Tree)	13.97	195.1			

(Feldhaar *et al*., 2000), and shared occupancy of individual arboreal domatia or nest sites by ant species has not been reported. One disadvantage to sharing shelters is a decrease in the fitness of a species through reduced pupal mass (Lill *et al*., 2007). However, co-habituation of nests by ant species could also be beneficial in that defence against mutual enemies is enhanced (Sagata *et al*., 2010). The *Crematogaster* and *Cataulacus* species were the only species with brood in the cocoons. The absence of brood in cocoons for the other morphospecies groups suggests that they are probably only using the cocoons opportunistically.

5.5.4 *Consequences for harvesting* G. postica

My results suggest that *G. postica* cocoons increase tree structural complexity and possibly species richness within trees as observed with other engineered structures (Martinsen *et al*., 2000; Lill & Marquis, 2003; Wang *et al*., 2012; Lima *et al*., 2013). The impact that an ecosystem engineer has depends on several factors, including the engineer's population density, the local and regional distribution of the engineer's population, the number of species that are dependent on the engineer, the resilience of the engineered structures and the length of time that the engineer's population is present in an area (Jones *et al*., 2004). Due to the sporadic nature of *Gonometa* populations through space and time (Veldtman *et al*., 2007), the exact spatial and temporal scale at which *G. postica*'s engineering effect operates is unknown. However, my results showed that several species occupied *G. postica* cocoons, with some using the cocoons to house brood. Furthermore, observations in the field suggest *G. postica* cocoons appear to persist for a long time within the trees in this environment. Therefore, at a local scale, *G. postica* appears to be acting as a potential autogenic ecosystem engineer (Jones *et al*., 1997) for the ants and other invertebrates on *V. erioloba,* despite the fact that certain ant species have displayed aggression towards foraging *G. postica* larvae on these trees (Campbell *et al*., 2013a).

Gonometa postica's role as an ecosystem engineer has implications for harvesting cocoons from the wild, though these implications may depend on the strength of the engineering effect. Currently, silk industries are reliant on harvesting empty *G. postica* cocoons, which, due to the unpredictable nature of *Gonometa* populations, are erratically available (Veldtman *et al*., 2002; Veldtman *et al*., 2007). My study showed that these same cocoons are also used secondarily by ants and other invertebrates as nesting or refuge sites. Whether or not this engineering effect extends across *G. postica*'s distributional range on all of its host trees, is unknown, though it has been observed in Namibia (pers. comm. Heather Campbell). Furthermore, I do not know the cocoon age at which ant occupancy first occurs.

Silk industries that rely on harvesting all empty cocoons from the trees could impact negatively on the ecosystem engineering effect created by *G. postica* for ants and other invertebrates. Removal of cocoons could result in a loss of ant colonies, which has been shown to result in severe myrmecophyte defoliation or mortality in other systems (Heil *et al*., 2001; Moraes & Vasconcelos, 2009) through the breakdown of mutualisms (Palmer *et al*., 2008). Moreover, depending on the strength of the ecosystem engineering effect, removal of all cocoons could have knock-on effects on ant-scale insect associations (Feldhaar *et al*., 2000).

I would suggest that silk industries, which utilize empty *G. postica* cocoons, harvest a proportion of these cocoons per tree, leaving some cocoons behind. This may allow the ecosystem engineering effect created by *G. postica* to be sufficiently maintained. My study showed that many of the *G. postica* cocoons were unoccupied by ants, suggesting that cocoons are not a limiting resource for the ants and that ants use these cocoons opportunistically. Alternatively, silk industries could look at harvesting emerged cocoons only because the ants in my study displayed a preference for cocoons containing parasite holes, though other invertebrates (which appear to frequently occupy emerged-only and/or cocoons with emergence and secondary holes) would also need to be considered. If cocoon collection cannot be regulated in this way to maintain the *G. postica* ecosystem engineering effect, the best option for silk industries would be to look at improving semi-captive and artificial rearing techniques. This will also allow silk industries to avoid the problems associated with using natural *Gonometa* populations. Lastly, further studies are needed to investigate the possible effects of cocoon presence on thorn domatia production by the host plants. There were no thorn domatia present on the trees sampled in this study; however, perhaps in the absence of *G. postica* cocoons, trees would produce domatia as a backup for anti-herbivore defence.

5.6 CONCLUSION

This study showed the importance of *G. postica* cocoons for providing shelter to ants and other invertebrates on *V. erioloba* trees. By increasing tree structural complexity and through variations in their characteristics, *G. postica* cocoons may promote co-existence between ants and other invertebrates (spiders, caterpillars and beetles) within individual *V. erioloba* trees. However, it is likely that these other invertebrates are also able to co-exist outside the cocoons. *Gonometa postica* cocoons appear to create new, favourable habitats for ants and other invertebrates on *V. erioloba*, making them autogenic ecosystem engineers in these systems. Cocoons can remain on these trees for multiple years; and, *G. postica* population outbreaks will create subsequent periods of greater cocoon availability. These factors could influence the duration and scale of the ecosystem engineering effect created by *G. postica*. Further studies would be required to determine the strength of the engineering effect created and the scales at which it operates.

CHAPTER 4

General Conclusion

The broad aim of this project was to contribute to current knowledge of two economically important silk moth species – *Gonometa postica* and *G. rufobrunnea* – to guide the potential future implementation of a sustainable silk harvesting industry in South Africa. Central to this research was the moth-host plant interaction, which was first examined at a large spatial scale, by investigating its importance (relative to climatic variables) in shaping *Gonometa* species distributions for southern and East Africa. Thereafter, we investigated a product of the moth-host plant interaction, i.e. *G. postica* cocoons, and the potential ecosystem engineering effect of *G. postica* cocoons on ants and other invertebrates in arboreal systems.

Species distribution modelling (SDM) was used to investigate the importance of the moth-host plant interaction in predicting *Gonometa* distributions at a large spatial scale. The general consensus from a majority of studies involving SDM is that climate is the main factor shaping species distributions; whereas, biotic interactions are considered as important mainly at local extents (Pearson & Dawson, 2003). However, more recently, studies have demonstrated the importance of biotic interactions in shaping species distributions at large spatial scales (e.g. Araújo & Luoto, 2007; Gilman *et al*., 2010). We therefore expected SDM performance to improve following the inclusion of moth-host plant interactions (i.e. by incorporating maps of host plant distributions as a proxy for the interactions into the models). On the contrary, we observed no improvement in SDM performance following the inclusion of moth-host plant interactions. Despite this, we found that the effect of host plant presence in shaping *Gonometa* species distributions could not be ignored because of its contribution to and importance in the models. The biotic (moth-host plant) models also differed from the abiotic models in their predictions of *Gonometa* species distributions, particularly into the future, and host plants could therefore potentially limit *Gonometa* species distributions. A review of SDM literature provided possible explanations for our unexpected results, revealing that the scales at which biotic interactions operate and their importance in shaping species distributions depend on the type of interactions involved (Araújo & Luoto, 2007; Preston *et al*., 2008; Van der Putten *et al*., 2010; Bateman *et al*., 2012) (e.g. positive consumer-resource interactions or negative competitive interactions) and the characteristics of species being modelled (Pöyry *et al*., 2008; Zurell *et al*., 2009; Schweiger *et al*., 2012). Furthermore, there is a possibility that different results would have been obtained if other factors (such as *Gonometa* species interactions with predators and parasitoids) were included into the models.

Gonometa species, through interactions with their host plants, also interact with other species. At a local spatial scale, the result of the moth-host plant interaction (i.e. cocoon production) appeared to benefit arboreal ants and other invertebrates associated with *Vachellia erioloba*. Thus, *G. postica*, via the cocoons that it spins acts as an autogenic ecosystem engineer, comparable to other arboreal ecosystem engineers such as leaf tying and leaf rolling caterpillars, leaf miners and stem boring beetles (Fukui, 2001; Lill & Marquis, 2003; Kagata & Ohgushi, 2004; Lima *et al*., 2013). Certain cocoon characters (i.e. cocoon size, entrance hole type and the presence of other invertebrate occupants within the cocoons) were related to ant presence and abundance within the cocoons and, although *G. postica* cocoons did not appear to be an essential resource to the ants, they probably created a more favourable environment for arboreal ants and other invertebrates based on their characteristics. Scale insect presence on the trees also significantly affected ant presence and abundance, which was expected because scale insects are a key resource for arboreal ants (Davidson *et al*. 2003). Furthermore, trees and cocoons were predominantly occupied by one ant species, but in some cases simultaneously by different ant species. Therefore, the moth-host plant interaction may be important for ant abundance, composition and coexistence in arboreal systems; although, further studies would be required to test this.

This study highlighted several key points that could be considered by silk industries. Firstly, climate and host plant distributions may both be important factors for defining *Gonometa* species distributions. To locate potential outbreak areas for cocoon collection, both factors need to be considered because *Gonometa* appear to be sensitive to climate, but are also dependent on their host plants (i.e. a food source) for survival. Personal observations revealed that *G. postica* showed a preference for one host tree species despite the presence of other hosts in the area. Therefore, future studies could investigate how the effect of variation (trait-based and chemical) within and between host plant species and individuals influences *Gonometa* preference and performance. More specifically, is there an “optimal tree” on which *G. postica* can be reared to maximize silk gains? Moreover, to improve semi-captive rearing techniques, future studies can test what the optimal herbivore loads are per tree, i.e. how will variation in the densities of *Gonometa* that are seeded onto trees impact on silk gains and the performance of the host trees involved.

Secondly, besides climate and host tree presence, other factors, such as predator and parasitoid abundances and distributions may be important factors shaping *Gonometa* species distributions. At my study site, 68% of the cocoons were parasitized (I Buyens *et al*., unpublished data). Based on this, and the unpredictable nature of *Gonometa* outbreaks, I think it would be more beneficial for silk industries to improve semi-captive rearing techniques (to optimize *Gonometa* survival and performance) than to rely on natural harvesting. To fully understand the role of a specific biotic interaction in shaping species distributions, an understanding of the species' ecology is required. For *Gonometa* species, studies addressing their ecology, particularly their interactions with their host plants and other species, are limited. Furthermore, of the studies involving *Gonometa* species, the majority have focussed on *G. postica*. Less work has been conducted on *G. rufobrummea* and its host plants, though *G. rufobrunnea* has also been used for commercial silk production. This provides an opportunity for future research.

Lastly, the potential of *G. postica* to influence ant and invertebrate species abundance, presence and coexistence indirectly through the production of cocoons (i.e. cocoons of different sizes, entrance hole types and sizes, hole numbers or even cocoon positions on the trees), yields potential implications for silk harvesting practices that are currently reliant on the collection of empty cocoons (which are able to persist on host trees for a long period of time following moth emergence, removal or death). However, to better understand the potential implications of cocoon removal on the ecosystem engineering effect created by *G. postica*, more research is required on the arboreal systems involved. Future studies could examine the microclimate created within the cocoons and compare this to the microclimate within thorn domatia and other arboreal structures that are used by ants and invertebrates.

Based on my results, it appears unlikely that cocoon harvesting will have a detrimental effect on the ants and other invertebrates because ants appear to use the cocoons opportunistically; however, the exact scales at which the engineering effect of *G. postica* operates and the magnitude of the effect is unknown. Therefore, studies are required to determine if *G. postica* acts as an autogenic ecosystem engineer across different spatial and temporal scales. Whether or not the created engineering effect is important enough to be affected by harvesting cocoons of natural populations (particularly for silk harvesting practices that use empty *G. postica* cocoons), and the effects of *Gonometa* species outbreaks hereon, needs to be assessed. If the magnitude of the ecosystem engineering effect is great, silk industries (that rely on the collection of empty cocoons) would need to take this into consideration and perhaps only harvest a proportion of the empty cocoons per tree. The knock-on effects of cocoon removal on other arboreal interactions in *Gonometa* host trees and on domatia production also needs to be assessed. To conclude, *Gonometa*-host plant interactions do not only play a role in shaping large-scale *Gonometa* species distributions, but may also play a role in the distribution and abundance of arboreal species at local scales.

REFERENCES

Abbott, K.C. & Dwyer, G. (2007) Food limitation and insect outbreaks: complex dynamics in plant–herbivore models. *Journal of Animal Ecology*, **76,** 1004−1014.

Agosta, J. (2006) On ecological fitting, plant-insect associations, herbivore host shifts, and host plant selection. *Oikos*, **114,** 556−565.

Akai, H. (1997) Anti-bacteria function of natural silk materials. *International Journal of Wild Silkmoth Silk,* **3,** 79–81.

Alalouni, U., Schädler, M. & Brandl, R. (2013) Natural enemies and environmental factors affecting the population dynamics of the gypsy moth. *Journal of Applied Entomology,* **137,** 721–738.

Ali, J.G. & Agrawal, A.A. (2012) Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science*, **17,** 293−302.

Arab, A. & Costa-Leonardo, A.M. (2005) Effect of biotic and abiotic factors on the tunneling behaviour of *Coptotermes gestroi* and *Heterotermes tenuis* (Isoptera: Rhinotermitidae). *Behavioural Processes,* **70,** 32–40.

Araújo, M.B., Cabeza§, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Climate Change Biology*, **10,** 1618−1626.

Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28,** 693–695.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33,** 1677–1688.

Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16,** 743–753.

Austin, M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, **157,** 101−118.

Bächtold, A., Alves-Silva, E., Kaminski, L.A. & Del-Claro, K. (2014) The role of tending ants in host plant selection and egg parasitism of two facultative myrmecophilous butterflies. *Naturwissenschaften*, **101,** 913–919.

Baek, H-J., Lee, J., Lee, H-S., Hyun, Y-K., Cho, C., Kwon, W-T., Marzin, C., Gan, S-Y., Kim, M-J., Choi, D-H., Lee, J., Lee, J., Boo, K-O., Kang, H-S. & Byun, Y-H. (2013) Climate change in the 21st century simulated by HadGEM2-AO under representative concentration pathways. *Asia-Pacific Journal of Atmospheric Sciences*, **49,** 603–618.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E., Harrington, R., Hartley, S., Jones, T.H., Lindroth, L.R., Press, M.C., Symrniodis, I., Watt, A.D. & Whittaker, J.B. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8,** 1−16.

Bandano, E. & Marquet, P.A. (2008) Ecosystem engineering affects ecosystem functioning in high-Andean landscapes. *Oecologia*, **4,** 821−829.

Banschbach, V.S., Levit, N. & Herbers, J.M. (1997) Nest temperatures and thermal preferences of a forest ant species: is seasonal polydomy a thermoregulatory mechanism? *Insectes Sociaux*, **44,** 109−122.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3,** 327–338.

Barry, S. & Elith, J. (2006) Error and uncertainty in habitat models. *Journal of Applied Ecology*, **43,** 413–423.

Bascompte, J. (2009) Mutualistic networks. *Frontiers in Ecology and the Environment*, **7,** 429–436.

Baselga, A. & Araújo, M.B. (2009) Individualistic vs community modelling of species distributions under climate change. *Ecography*, **32,** 55–65.

Bateman, B.L., VanDerWal, J., Williams, S.E. & Johnson, C.N. (2012) Biotic interactions influence the projected distribution of a specialist mammal under climate change. *Diversity and Distributions*, **18,** 861−872.

Beattie, A.J., & Hughes, L. (2002) Ant–plant interactions. In: Herrera CM, Pellmyr O (eds) Plant–animal interactions: an evolutionary approach. Blackwell Science, Oxford, pp 211–235.

Beaumont, L.J. & Hughes, L. (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology*, **8,** 954−971.

Berryman, A. A. (1996) What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution*, **11,** 28−32.

Blatrix, R., Bouamer, S., Morand, S. & Selosse, M-A. (2009) Ant-plant mutualisms should be viewed as symbiotic communities. *Plant Signalling & Behavior*, **4,** 554−556.

Blois, J.L., Zarnetske, P.H., Fitzpatrick, M.C. & Finnegan, S. (2013) Climate change and the past, present, and future of biotic interactions. *Science*, **341,** 499−504.

Blüthgen, N. & Fiedler, K. (2002) Interactions between weaver ants (*Oecophylla smaragdina*), homopterans, trees and lianas in an Australian rainforest canopy. *Journal of Animal Ecology*, **71,** 793–801.

Blüthgen, N., Stork, N.E. & Fiedler, K. (2004) Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos,* **106,** 344–358.

Blüthgen, N. & Feldhaar, H. (2010) Food and shelter: how resources influence ant ecology. In: Lach L, Parr C, Abbott K. eds. Ant ecology. Oxford: Oxford University Press, 115–136.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.E., Poulsen, J.R., Stevens, M.H.H. & White, J-S.S. (2008) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24,** 127−135.

Boulangeat, I. Gravel, G. & Thuiller, W. (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, **15,** 584–593.

Braschler, B. & Hill, J.K. (2007) Role of larval host plants in the climate-driven range expansion of the butterfly *Polygonia c-album. Journal of Animal Ecology*, **76,** 415−423.

Breitburg, D.L., Crump, D.C., Dabiri, J.O. & Gallegos, C.L. (2010) Ecosystem engineers in the pelagic realm: alteration of habitat by species ranging from microbes to jellyfish. *Integrative and Comparative Biology*, **50,** 188−200.

Bronstein, J.L. (1998). The contribution of ant-plant protection studies to our understanding of mutualism. *Biotropica,* **30,** 150–161.

Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245,** 59–65.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18,** 119–125.

Campbell, H., Townsend, L.R., Fellowes, M.D.E. & Cook, J.M. (2013a) Thorn-dwelling ants provide antiherbivore defence for camelthorn trees, *Vachellia erioloba*, in Namibia. *African Journal of Ecology*, **51,** 590–598.

Campbell, H., Townsend, L.R., Fellowes, M.D.E. & Cook, J.M. (2013b) Arboreal thorn-dwelling ants coexisting on the savannah ant-plant, *Vachellia erioloba*, use domatia morphology to select nest sites. *Insectes Sociaux*, **60,** 373–382.

Carey, P.D. (1996) DISPERSE: a cellular automaton for predicting the distribution of species in a changed climate. *Global Ecology and Biogeography Letters*, **5,** 217– 226.

Case, T.J., Holt, R.D., McPeek, M.A. & Keitt, T.H. (2005) The community context of species' borders: ecological and evolutionary perspectives. *Oikos*, **108,** 28−46.

Catana, A.J. Jr. (1963) The wandering quarter method of estimating population density. *Ecology*, **44,** 349–360.

Chen, I-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333,** 1024–1026.

Chikwenhere, G. P. (1992) Distribution and abundance of the African silkmoth (*Gonometa rufobrunnea*) in Matebeleland Province of Zimbabwe. *Zimbabwe Journal of Agricultural Research*, **29,** 133–137.

Collier, P., Conway, G. & Venables, T. (2008) Climate change and Africa. *Oxford Review of Economic Policy*, **24,** 337−353.

Dangerfield, J.M., McCarthy, T.S. & Ellery, W.N. (1998) The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology*, **14,** 507−520.

Davidson, D.W. & McKey, D. (1993) The evolutionary ecology of symbiotic ant-plant relationships. *Journal of Hymenoptera Research*, **2,** 13–83.

Davidson, D. W., Cook, S. C., Snelling, R. R. & Chua, T.H. (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, **300,** 969–972.

Dean, W., Milton, S. & Jeltsch, F. (1999) Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments*, **41,** 61–78.

Dejean, A., Djiéto-Lordon, C. & Orivel, J. (2008) The plant ant *Tetraponera aethiops* (Pseudomyrmecinae) protects its host myrmecophyte *Barteria fistulosa* (Passifloraceae) through aggressiveness and predation. *Biological Journal of the Linnean Society*, **93,** 63–69.

Dejean, A., Fisher, B.L., Cobara, B., Rarevohitra, R., Rajemison, B. & Leponse, M. (2010) Spatial distribution of dominant arboreal ants in a Malagasy Coastal Rainforest: gaps and presence of invasive species. *PLoS ONE*, **7,** e9319.

Dejean, A., Delabie, J.C.H., Cobara, B., Azemar, F., Groc, S., Orivel, J. & Leponse, M. (2012) The ecology and feeding habits of the arboreal trap-jawed ant *Daceton armigerum*. *PLoS ONE*, **7,** e37683.

Delport, W. (2006) Population genetic inference of demographic processes in the African Wild Silk Moth, *Gonometa postica* (Lasiocampidae). PhD thesis, University of Pretoria, South Africa.

Dufresne, J-L., Foujols, M-A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H., Benshila, R., Bony, S., Bopp, L., Braconnot, P., Brockmann, P., Cadule, P., Cheruy, F., Codron, F., Cozic, A., Cugnet, D., de Noblet, N., Duvel, J-P., Ethé, C., Fairhead, L., Fichefet, T., Flavoni, S., Friedlingstein, P., Grandpeix, J-Y., Guez, L., Guilyardi, E., Hauglustaine, D., Hourdin, F., Idelkadi, A., Ghattas, J., Joussaume, S., Kageyama, M., Krinner, G., Labetoulle, S., Lahellec, A., Lefebvre, M-P., Lefevre, F., Levy, C., Lee, Z.X., Lloyd, J., Lott, ., Madec, G., Mancip, M., Marchand, M., Masson, S., Meurdesoif, Y., Mignot, J., Musat, I., Parouty, S., Polcher, J., Rio, C., Schulz, M., Swingedouw, D., Szopa, S., Talandier, C., Terray, P., Viovy, N. & Vuichard, N. (2013) Climate change projections using the IPSL-CM5 earth system model: from CMIP3 to CMIP5. *Climate Dynamics*, **40,** 2123–2165.

Edwards, D.P., Frederickson, M.E., Shepard, G.H. & Yu, D.W. (2009) A plant needs ants like a dog needs fleas: *Myrmelachista schumanni* ants gall many tree species to create housing. *The American Naturalist*, **174,** 734–740.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Soberón, J., Williams, S., Wisz, M. S. & Zimmermann, N. E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29,** 129–151.

Elith, J. & Leathwick, J. (2007) Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions*, **13,** 265–275.

Elith, J. & Graham, C.H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32,** 66−77.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40,** 677−697.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17,** 43−57.

Elith, J. & Franklin, J. (2013) Species distribution modelling. Encyclopaedia of Biodiversity (ed.by S. Levin), pp. 692−705. Academic Press, Waltham, MA.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. & Wessels, K.J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology*, **8,** 679–693.

Eskildsen, A., le Roux, P.C., Heikkinen, R.K., Høye, T.T., Kissling, W.D., Pöyry, J., Wisz, M.S. & Luoto, M. (2013) Testing species distribution models across space and time: high latitude butterflies and recent warming. *Global Ecology and Biogeography*, **22,** 1293−1303.

Federle, W., Brainerd, E.L., McMahon, T.A., Hölldobler, B. (2001) Biomechanics of the movable pretarsal adhesive organ in ants and bees. *Proceedings of the National Academy of Science*, **98,** 6215–6220.

Feldhaar, H., Fiala, B., bin Hashim, R. & Maschwitz, U. (2000) Maintaining an ant-plant symbiosis: secondary polygyny in the *Macaranga triloba-Crematogaster* sp. association, *Naturwissenschaften*, **87,** 408–411.

Fening, K.O. (2008) Spatial distribution and biology of *Gonometa postica* Walker (Lepidoptera: Lasiocampidae) with reference to its key parasitoids on Acacia species in Mwingi, Kenya. PhD Thesis, Kenyatta University, Nairobi.

Fening, K.O., Kioko, E.N., Raina, S.K. & Mueke, J.M. (2008) Monitoring wild silkmoth, *Gonometa postica* Walker, abundance, host plant diversity and distribution in Imba and Mumoni woodlands in Mwingi, Kenya. *International Journal of Biodiversity Science and Management,* **4,** 104–111.

Fening, K.O., Kioko, E.N., Raina, S.K. & Mueke, J.M. (2009) Parasitiods of the African wild silkmoth, *Gonometa postica* (Lepidoptera: Lasiocampidae) in the Mwingi forests, Kenya. *Journal of Applied Entomology*, **133,** 411–415.

Fening, K.O., Kioko, E.N., Raina, S.K. & Mueke, J.M. (2010) Effects of seasons and larval food plants on the quality of *Gonometa postica* cocoons. *Phytoparasitica*, **38,** 111–119.

Fening, K.O., Kioko, E.N., Mueke, J.M. & Raina, S.K. (2011) Oviposition preferences of the African Wild Silkmoth, *Gonometa postica* Walker (Lepidoptera: Lasiocampidae) on different substrates. *Journal of Insect Behaviour*, **24,** 1−10.

Ferguson, J.W.H. & Wilson, T. (2011) The suitability of the African silk moth *Gonometa postica* as a sustainable resource for the production of silk. A report prepared for the CSIR. Centre for Environmental Studies, University of Pretoria.

Fiedler, K. & Maschwitz, U. (1989) The symbiosis between the weaver ant, *Oecophylla smaragdina*, and *Anthene emolus*, an obligate myrmecophilous lycaenid butterfly. *Journal of Natural History*, **23,** 833−846.

Fiedler, K.O. (2006) Ant-associates of Palaearctic lycaenid butterfly larvae (Hymenoptera: Formicidae; Lepidoptera: Lycaenidae) – a review. *Myrmecologische Nachrichten,* **9,** 77−87.

Fincke, O.M. (1999) Organisation of predator assemblages in neotropical tree holes: effects of abiotic factors and priority. *Ecological Entomology,* **24,** 13–23.

Fonseca, C.R. (1999) Amazonian ant–plant interactions and the nesting space limitation hypothesis. *Journal of Tropical Ecology,* **13,** 807−825.

Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P. & Shapiro, A.M. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *PNAS,* **107,** 2088–2092.

Fournier, V., Rosenheim, J.A., Bordeur, J., Laney, L.O. Johnson, M.W. (2003) Herbivorous mites as ecological engineers: indirect effects on arthropods inhabiting papaya foliage. *Oecologia*, **135,** 442–450.

Freddi, G., Bianchi Svilokos, A., Ishikawa, H., Tsukada, M. (1993) Chemical composition and physical properties of *Gonometa rufobrunnea* silk. *Journal of Applied Polymer Science,* **48,** 99–106.

Fukui, A. (2001) Indirect interactions mediated by leaf shelters in animal–plant communities. *Population Ecology,* **43,** 31−40.

Giannini, T.C., Chapman, D.S., Saraiva, A.M., Alves-dos-Santos, I. & Biesmeijer, J.C. (2013) Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants. *Ecography,* **36,** 649−656.

Gibbs, H. & Cunningham, S.A. (2009) Does the availability of arboreal honeydew determine the prevalence of ecologically dominant ants in restored habitats? *Insectes Sociaux,* **56,** 405−412.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution*, **25,** 325–331.

Godsoe, W. & Harmon, L.J. (2012) How do species interactions affect species distribution models? *Ecography,* **35,** 811–820.

Gould, J.R., Elkinton, J.S. & Wallner, W.E. (1990) Density-dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. *Journal of Animal Ecology,* **59,** 213–233.

Graham, C.H., Elith, J., Hijmans, R.J., Guisan, A., Peterson, A.T., Loiselle, B.A. & The Nceas Predicting Species Distributions Working Group. (2008) The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology*, **45,** 239–247.

Greve, M., Lykke, A.M., Fagg, C.W., Bogaert, J., Friis, I., Marchant, R., Marshall, A.R., Ndayishimiye, J., Sandel, B.S., Sandom, C., Schmidt, M., Timberlake, J.R., Wieringa, J.J., Zizka, G. & Svenning, J-C. (2012) Continental-scale variability in browser diversity is a major driver of diversity patterns in acacias across Africa. *Journal of Ecology,* **100,** 1093−1104.

Guido, M. & Gianelle, D. (2001) Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. *Acta Oecologia*, **22,**175−185.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135,** 147−186.

Guisan, A.T. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8,** 993−1009.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J. MC.C., Aspinall, R. & Hastie, T. (2006) Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology*, **43,** 386–392.

Guitiérrez, J.L., Jones, C.J., Strayer, D.L. & Iribarne, O.O. (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, **101,** 79–90.

Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology,* **143,** 29–36.

Hanspach, J., Kühn, I., Pompe, S. & Klotz, S. (2010) Predictive performance of plant species distribution models depends on species traits. *Perspectives in Plant Ecology, Evolution and Systematics*, **12,** 219–225.

Hartland-Rowe, R. (1992) The biology of the wild silkmoth *Gonometa rufobrunnea* Aurivillius (Lasiocampidae) in northeastern Botswana, with comments on its potential as a source of wild silk. *Botswana Notes and Records*, **24,** 123–133.

Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.J., Lambrinos, J.G., Talley, T.S. & Wilson, W.G. (2007) Ecosystem engineering in space and time. *Ecology Letters*, **10,** 153–164.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84,** 3105–3117.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Köber, J-H. (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography*, **16,** 754−763.

Heil, M., B. Fiala, Maschwitz, U., & Linsenmair, K.E. (2001) On the benefits of indirect defence: short- and long-term studies in antiherbivore protection via mutualistic ants. *Oecologia*, **126,** 395–403.

Heil, M. & McKey, D. (2003) Protective ant-plant interactions as model systems in ecological an evolutionary research. *Annual Review of Ecology, Evolution and Systematics*, **34,** 425−453.

Heil, M., González-Teuber, M., Clement, L.W., Kautz, S., Verhaagh, M., Bueno, J.C.S. (2009) Divergent investment strategies of *Acacia* myrmecophytes and the coexistence of mutualists and exploiters. *PNAS*, **106,** 18091–18096.

Hengl, T., Mendes de Jesus. J., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B.M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J.G.B., Walsh, M.G. & Gonzalez, M.R. (2014) SoilGrids1km — Global Soil Information Based on Automated Mapping. *PLoS ONE*, **9,** 1−17.

Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29,** 773−785.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25,** 1965–1978.

Hood, W.G. & Tschinkel, W.R. (1990) Desiccation resistance in arboreal and terrestrial ants. *Physiological Entomology*, **15,** 23–25.

Hughes, L. (2000) Biological consequences of global warming: is the signal already. *Trends in Ecology and Evolution*, **15,** 56−61.

Hunter, A.F. & Lechowicz, M.J. (1992) Foliage quality changes during canopy development of some northern hardwood trees. *Oecologia*, **89,** 316–323.

Hunter, A.F. & Elkinton, J.S. (2000) Effects of synchrony with host plant on populations of a spring-feeding lepidopteran. *Ecology,* **81,** 1248−1261.

Huntley, B.J. & Walker, B.H. (1982) *Ecology of Tropical Savannas*. New York: Springer-Verlag, Berlin.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland.

James, R., Washington, R. & Rowell, D.P. (2014) African climate change uncertainty in perturbed physics ensembles: implications of global warming to 48°C and beyond. *American Meteorological Society*, **27,** 4677–4692.

Jamieson, M.A., Trowbridge, A.M., Raffa, K.F. & Lindroth, R.L. (2012) Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, **160,** 1719−1727.

Jeffries, M.J. & Lawton, J.H. (1984) Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23,** 269–286.

Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, **14,** 885–890.

Jones, C.G., Lawton, J.H. & Shachak, M (1994) Organisms as ecosystem engineers. *Oikos*, **69,** 373–86.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78,** 1946–1957.

Jones, C.G., Guitiérrez, J.L, Groffman, P.M. & Shachak, M. (2006) Linking ecosystem engineers to soil processes: a framework using the Jenny State Factor Equation. *European Journal of Soil Biology,* **42,** S39−S53.

Jones, J.C. & Oldroyd, B.P. (2007) Nest thermoregulation in social insects. *Advances in Insect Physiology*, **33,** 153–191.

Jones, C., Hughes, J.K., Bellouin, N., Hardiman, S.C., Jones, G.S., Knight, H., Liddicoat, S., O'Connor, F.M., Andres, R.G., Bell, C., Boo, K-O., Bozzo, A., Butchart, N., Cadule, P., Corbin, K.B., Doutriaux-Boucher, M., Friedlingstein, P., Gornall, J., Gray, L., Halloran, P.R., Hurtt, G., Ingram, W.J., Lamarque, J-F., Law, R.M., Meinshausen, M., Osprey, S., Palin, E.J., Parsons Chini, L., Raddatz, T., Sanderson, M.G., Sellar, A.A., Schurer, A., Valdes, P., Wood, N., Woodward, S., Yoshioka, M. & Zerroukat, M. (2011), The HadGEM2-ES implementation of CMIP5 centennial simulations. *Geoscientific Model Development*, **4,** 543–570.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P. & Lepage, M. (2006) Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology*, **32,** 153–164.

Kagata, H. & Ohgushi, T. (2004) Leaf miner as a physical ecosystem engineer: secondary use of vacant leaf mines by other arthropods. *Annals of the Entomological Society of America*, **97,** 923–927.

Kaminski, L.A., Freitas, A.V.L. & Oliveira, P.S. (2010) Interaction between Mutualisms: Ant-Tended Butterflies Exploit Enemy-Free Space Provided by Ant-Treehopper Associations. *The American Naturalist*, **176,** 322–334.

Kaminski, L.A. & Roderigues, D. (2011) Species-specific levels of ant attendance mediate performance costs in a facultative myrmecophilous butterfly. *Physiological Entomology*, **36,** 208–214.

Kawai, T. & Tokeshi, M. (2006) Asymmetric coexistence: bidirectional abiotic and biotic effects between goose barnacles and mussels. *Journal of Animal Ecology*, **75,** 928−941.

Kearney, M. (2006) Habitat, environment and niche: what are we modelling? *Oikos*, **115,** 186–191.

Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12,** 334–350.

Kelley, S.T. & Farrell, B.D. (1998) Is Specialization a Dead End? The phylogeny of host use in dendroctonus bark beetles (Scolytidae). *Evolution*, **52,** 1731–1743.

Keppel, G., Van Niel, K.P., Warell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D. & Franklin, S.E. (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, **21,** 393–404.

Kioko, E.N., Raina, S.K. & Mueke, J.M. (2000) Survey on the diversity of wild silk moth species in East Africa. East African *Journal of Science*, **2,** 1–6.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J., Montoya, J.M., Römermann, C., Schiffers, K., Schurr, F.M., Singer, A., Svenning, J-C., Zimmermann, N.E. & O'Hara, R.B. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, **39,** 2163−2178.

Klemola, N., Andersson, T., Ruohomäki, K. & Klemola, T. (2010) Experimental test of parasitism hypothesis for population cycles of a forest lepidopteran. *Ecology*, **91,** 2506–2513.

Klemola, T., Andersson, T. & Ruohomäki, K. (2014) Delayed density‐dependent parasitism of eggs and pupae as a contributor to the cyclic population dynamics of the autumnal moth. *Oecologia*, **175,** 1211−1225.

Knobel, J & Bredenkamp, G. (1999) The magnificent natural heritage of South Africa. Sunbird Publishers, Roggebaai, pp. 10−25.

Kroon, D.M. (1999) Lepidoptera of Southern Africa: Host–Plants and Other Associations, A catalogue. Lepidopterists' Society of Africa, Salisburgtd.

le Roux, P.C., Virtanen, R., Heikkinen, R.K. & Luoto, M. (2012) Biotic interactions affect the elevational ranges of high-latitude plant species. *Ecography*, **35,** 1048−1056.

Leathwick, J.R. & Austin, M.P. (2001) Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology*, **82,** 2560–2573.

Leathwick, J.R. (2002) Intra-generic competition among *Nothofagus* in New Zealand's primary indigenous forests. *Biodiversity and Conservation*, **11,** 2117–2187.

Leroy, C., Jauneau, A., Quilichini, A., Dejean, A. & Orivel, J. (2010) Comparative structure and ontogeny of the foliar domatia in three neotropical myrmecophytes. *American Journal of Botany*, **97,** 557−565.

Liebhold, A., Elkinton, J., Williams, D. & Muzika, R-M. (2000) What causes outbreaks of the gypsy moth in North America? *Population Ecology*, **42,** 257−266.

Lill, J.T. & Marquis, R.J. (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology*, **84,** 682−690.

Lill, J.T. & Marquis, R.J. (2004) Leaf ties as colonization sites for forest arthropods: an experimental study. *Ecological Entomology*, **29,** 300−308.

Lill, J.T., Marquis, R.J., Walker, M.A. & Peterson, L. (2007) Ecological consequences of shelter sharing by leaf-tying caterpillars. *Entomologia Experimentalis et Applicata*, **124,** 45–53.

Lima, V.O., Demite, P.R., Vieira, C., Feres, R.J.F. & Romero, G.Q. (2013) Contrasting engineering effects of leaf-rolling caterpillars on a tropical mite community. *Ecological Entomology*, **38,** 193–200.

Logan, J.A., Regniere, J. & Powell, J.A. (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, **1,** 130–137.

Lovett, G.M, Christenson, L.M, Groffman, P.M, Jones, C.G, Hart, J.E, Mitchell, M.J. (2002) Insect defoliation and nitrogen cycling in forests. *Bioscience*, **52,** 335–341.

Lovett, J.C. (2015) Modelling the effects of climate change in Africa. *African Journal of Ecology*, **53,** 1–2.

Lumsden, T.G., Schulze, R.E. & Hewitson, B.C. (2009) Evaluation of potential changes in hydrologically relevant statistics of rainfall in Southern Africa under conditions of climate change. *Water SA*, **35,** 649–656.

Luoto, M., Pöyry, J., Heikkinen, R.K. & Saarinen, K. (2005) Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Global Ecology and Biogeography* **14,** 575–584.

Mallon, E.B., Pratt, S.C. & Franks, N.R. (2001) Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behavioural Ecology and Sociobiology*, **50,** 352–359.

Maron, J.L., Harrison, S. & Greaves, M. (2001) Origin of an insect outbreak: escape in space or time from natural enemies? *Oecologia*, **126,** 595−602.

Martin, T.E. (2001) Abiotic vs. biotic influences on habitat selection of co-existing species: climate change impacts? *Ecology*, **82,** 175–188.

Martins, D.J., Collins, S.C., Congdon, C. & Pierce, N.E. (2013) Association between the African lycaenid, *Anthene usamba*, and an obligate acacia ant, *Crematogaster mimosa*. *Biological Journal of the Linnean Society*, **109,** 302–312.

Martinsen, G.D., Floate, K.D., Waltz, A.M., Wimp, G.M. & Whitham, T.G. (2000) Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia*, **123,** 82−89.

Mayer, V.E., Frederickson, M.E., McKey, D. & Blatrix, R. (2014) Current issues in the evolutionary ecology of ant–plant symbioses. *New Phytologist*, **202,** 749–764.

McGeoch, M.A. (2000) View from the frontline: insect conservation in South Africa. *Antenna*, **25,** 21–32.

McGeoch, M.A. (2002) Insect conservation in South Africa: an overview. African *Entomology*, **10,** 1 – 10.

McKey, D. (1984) Interaction of the ant-plant *Leonardoxa africana* (Caesalpiniaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica*, **16,** 81−99.

McMillin, J.D. & Wagner, M.R. (1998) Influence of host plant vs. natural enemies on the spatial distribution of a pine sawfly, *Neodiprion autumnalis*. *Ecological Entomology*, **23,** 397–408.

McPherson, J.M. & Jetz, W. (2007) Effects of species' ecology on the accuracy of distribution models. *Ecography*, **30,** 135−151.

Meier, S.M., Kienast, F., Pearman, P.B., Svenning, J-C., Thuiller, W., Araújo, M.B, Guisan, A. & Zimmermann, N.E. (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, **33,** 1038–1048.

Meier, E.S., Edwards Jr., T.C., Kienast, F., Dobbertin, M. & Zimmermann, N.E. (2011) Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, **38,** 371−382.

Menéndez, R. (2007) How are insects responding to global warming? *Tijdschrift voor Entomologie*, **150,** 355–365.

Menéndez, R., González-Megías, A., Collingham, Y., Fox, R., Roy, D.B., Ohlemüller, R. & Thomas, C.D. (2007) Direct and indirect effects of climate and habitat factors on butterfly diversity. *Ecology*, **88,** 605−611.

Merow, C., Smith, M.J. & Silander Jr., J.A. (2013) A practical guide to MaxEnt for modelling species distributions: what it does, and why inputs and settings matter. *Ecography*, **36,** 1058–1069.

Midgley, G.F., Hannah, L., Millar, D., Thuiller, W. & Booth, A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, **112,** 87–97.

Midgley, G.F. & Thuiller, W. (2011) Potential responses of terrestrial biodiversity in Southern Africa to anthropogenic climate change. *Regional Environmental Change*, **11,** 127–135.

Moraes, S.C. & Vasconcelos, H.L. (2009) Long-term persistence of a Neotropical ant-plant population in the absence of obligate plant-ants. *Ecology*, **90,** 2375–2383.

Morán-Ordóñez, A., Suáerz-Seoane, S., Elith, J., Calvo, L. & de Luis, E. (2012) Satellite surface reflectance improves habitat distribution mapping: a case study on heath and shrub formations in the Cantabrian Mountains (NW Spain). *Diversity and Distributions*, **18,** 588−602.

Nakamura, M. & Ohgushi, T. (2003) Positive and negative effects of leaf shelters on herbivorous insects: linking multiple herbivore species on a willow. *Oecologia*, **136,** 445−449.

Nelson, W.A., Bjørnstad, O.N. & Yamanaka, T. (2013) Recurrent Insect outbreaks caused by temperature-driven changes in system stability. *Science*, **314,** 796–799.

Ngoka, B.M., Kioko, E.N., Raina, S.K., Mueke, J.M. & Kimbu, D.M. (2008) Semi-captive rearing of the African Wild Silkmoth *Gonometa postica* (Lepidoptera: Lasiocampidae) on an indigenous and a non-indigenous host plant in Kenya. *International Journal of Tropical Insect Science*, **27,** 183–190.

Östergård, H. & Ehrlén, J. (2005) Among population variation in specialist and generalist seed predation – the importance of host plant distribution, alternative hosts and environmental variation. *Oikos*, **111,** 39–46.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14,** 483–488.

Palmer, T.M., Young, T.P., Stanton, M.L. & Wenk, E. (2000) Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia*, **123,** 425–435.

Palmer, T. M., Young, T. P. & Stanton, M.L. (2002) Burning bridges: priority effects and the persistence of a competitively subordinate acacia-ant in Laikipia, Kenya. *Oecologia*, **133,** 372–379.

Palmer, T.M. (2003) Spatial habitat heterogeneity influences competition and coexistence in an African acacia ant guild. *Ecology*, **84,** 2843–2855.

Palmer, T.M. (2004) Wars of attrition: colony size determines competitive outcomes in a guild of African acacia ants. *Animal Behaviour*, **68,** 993–1004.

Palmer, T.M., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M. & Karban, R. (2008) Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science*, **319,** 192–195.

Palmer, T., Doak, D.F., Stanton, M.L., Bronstein, J.L., Kiers, E.T., Young, T.P., Goheen, J.R. & Pringle, R.M. (2010) Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *PNAS*, **107,** 17234–17239.

Palmer, T.M. & Brody, A.K. (2013) Enough is enough: the effects of symbiotic ant abundance on herbivory, growth, and reproduction in an African acacia. *Ecology*, **94,** 683–691.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 578–583.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics,* **37,** 637−669.

Partridge, L.W., Partridge, K.A. & Franks, N.R. (1997) Field survey of a monogynous leptothoracine ant (Hymenoptera, Formicidae): evidence of seasonal polydomy? *Insectes Sociaux,* **44,** 75–83.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography,* **12,** 361–371.

Pellissier, L., Bråthen, K.A., Pottier, J., Randin, C.F., Vittoz, P., Dubuis, A., Yoccoz, N.G., Alm, T., Zimmermann, N.E. & Guisan, A. (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography,* **33,** 1004−1014.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190,** 231−259.

Phillips, S. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31,** 161−175.

Pierce, N.E. (1995) Predatory and parasitic Lepidoptera: carnivores living on plants. *Journal of the Lepidopterists' Society,* **49,** 412-453.

Porter, S.D. (1988) Impact of temperature on colony growth and developmental rates of the ant, *Solenopsis invicta*. *Journal of Insect Physiology*, **34,** 1127−1133.

Powell, S. (2009) How ecology shapes caste evolution: linking resource use, morphology, performance and fitness in a superorganism. *Journal of Evolutionary Biology,* **22,** 1004–1013.

Powell, S., Costa, A.N., Lopes, C.T. & Vasconcelos, H. L. (2011) Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. *Journal of Animal Ecology*, **80,** 352−360.

Pöyry, J., Luoto, M., Heikkinen, R.K. & Saarinen, K. (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography,* **17,** 403−414.

Pratt, S.C. & Pierce, N.E. (2001) The cavity-dwelling ant *Leptothorax curvispinosus* use nest geometry to discriminate between potential homes. *Animal Behaviour*, **62,** 281–287.

Pratt, S.C., Mallon, E.B., Stumpter, D.J.T. & Franks, N.R. (2002) Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behavioural Ecology and Sociobiology*, **52,** 117–127.

Preston, K.L., Rotenberry, J.T., Redak, R.A. & Allen, M.F. (2008) Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. *Global Change Biology*, **14,** 2501–2515.

Pringle, E.G., Dirzo, R. & Gordon, D.M. (2011) Indirect benefits of symbiotic coccoids for an ant-defended myrmecophytic tree. *Ecology*, **91,** 37–46.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3,** 349–361.

Raine, N.E., Gammans, N., Macfadyen, I.J., Scriver, G.K. & Stone, G.N. (2004) Guards and thieves: antagonistic interactions between two ant species co-existing on the same ant-plant. *Ecological Entomology*, **29,** 345–352.

Ringler, C., Zhu, T., Cai, X., Koo, J. & Wang, D. (2010) Climate change impacts on food security in sub-Saharan Africa: Insights from comprehensive climate change scenarios. IFPRI discussion paper 01042.

Ritchie, E.G., Martin, J.K., Johnson, C.N. & Fox, B.J. (2009) Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores. *Journal of Animal Ecology*, **78,** 724–731.

Roces, F. & Núñez, A. (1989) Brood translocation and circadian variation of temperature preference in the ant *Camponotus mus*. *Oecologia*, **81,** 33–37.

Roland, J. (1993) Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93,** 25–30.

Rose, C.E., Martin, S.W., Wannemuehler, K.A. & Plikaytis, B.D. (2006) On the use of zero-inflated and hurdle models for modeling vaccine adverse event count data. *Journal of Biopharmaceutical Statistics*, **16,** 463–481.

Rosumek, F.B., Silveira, F.A.O., Neves, F.D.S., Newton, P.D.U.B., Diniz, L., Oki, Y., Pezzini, F., Fernandes, G.W. & Cornelissen, T. (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, **160,** 537–549.

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6,** 407–416.

Sagata, K., Mack, A.L. Wright, D.D. & Lester, P.J. (2010) The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. *Insectes Sociaux*, **57,** 333−341.

Schmitz, O.J., Hambäck, P.A. & Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist*, **155,** 141–153.

Scholtz, C.H. & Holm, E. (1985) Insects of Southern Africa. University of Pretoria, Pretoria.

Schultz, J.C. (1992) Factoring natural enemies into plant tissue availability to herbivores. Effects of Resource Distribution on Animal–Plant Interactions (ed. by M. D. Hunter, T. Ohgushi and P. W. Price), pp. 175–198. Academic Press, San Diego, California.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kühn, I. (2008) Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, **89,** 3472−3479.

Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry, J. & Settele, J. (2012) Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography*, **21,** 88−99.

Seymour, C. & Milton, S. (2003) A collation and overview of research information on *Acacia erioloba* (Camelthorn) and identification of relevant research gaps to inform protection of the species. Department of Water Affairs and Forestry, Pretoria.

Shenoy, M. & Borges, R.M. (2008) A novel mutualism between an ant-plant and its resident pollinator. *Naturwissenschaften*, **95,** 61–65.

Shenoy, M. & Borges, R.M. (2010) Geographical variation in an ant–plant interaction correlates with domatia occupancy, local ant diversity, and interlopers. *Biological Journal of the Linnean Society*, **100,** 538–551.

Smith, T.M. & Goodman, P.S. (1986) Successional dynamics in an *Acacia nilotica-Euclea divinorum* savannah in southern Africa. *Journal of Ecology*, **75,** 603–610.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10,** 1115–1123.

Soliveres, S., Maestre, F.T., Berdugo, M. & Allan, E. (2015) A missing link between facilitation and plant species coexistence: nurses benefit generally rare species more than common ones. *Journal of Ecology*, **103,** 1183−1189.

Stachowicz, J.J. (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, **51,** 235−246.

Stanton, M.L., Palmer, T.M., Young, T.P., Evans, A. & Turner, M.L. (1999) Sterilization and canopy modification of a swollen thorn Acacia tree by a plant–ant. *Nature*, **401,** 578–581.

Stanton, M.L. & Palmer, T.P. (2011) The high cost of mutualism: effects of four species of East African ant symbionts on their myrmecophyte host tree. *Ecology*, **92,** 1073–1082.

Stapley, L. (1998) The interaction of thorns and symbiotic ants as an effective defence mechanism of swollen-thorn acacias. *Oecologia*, **115,** 401–405.

Stefanescu, C., Peñuelas, J. & Filella, L. (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9,** 1494–1506.

Stefanscu, C., Carnicer, J. & Peñuelas, J. (2011) Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography*, **34,** 353–363.

Stockwell, D.RB. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **149,** 1−13.

Styrsky, J.D. & Eubanks, M.D. (2007) Ecological consequences of interactions between ants and honeydew-producing insects. *Proceedings of the. Royal Society of London, B,* **274,** 151–164.

Styrsky, J.D. (2014) An orb-weaver spider exploits an ant–acacia mutualism for enemy-free space. *Ecology and Evolution*, **4,** 276– 283.

Syphard, A.D. & Franklin, J. (2010) Species traits affect the performance of species distribution models for plants in southern California. *Journal of Vegetation Science*, **21,** 177−189.

Tadross, M.A., Jack, C. & Hewitson, B.C. (2005) On RCM-based projections of change in southern African summer climate. *Geophysical Research Letters*, **32,** L23713, doi 10.1029/200.

Tamburini, G., Marini, L., Hellrigl, K., Salvadori, C. & Battiste, A. (2013) Effects of climate and density-dependent factors on population dynamics of the pine processionary moth in the Southern Alps. *Climate Change*, **121,** 701−712.

Tanaka, H.O., Yamane, S. & Itioka, T. (2010) Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. *Population Ecology,* **52,** 147−157.

Thomas, M.L. (2002) Nest site selection and longevity in the ponerine ant *Rhytidoponera metallica* (Hymenoptera, Formicidae). *Insectes Sociaux*, **49,** 147–152.

Thuiller, W., Lavorel, S., Araújo, M.B., Skyes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *PNAS*, **102,** 8245−8250.

Tirado, R. & Pugnaire, F.I. (2005) Community structure and positive interactions in constraining environments. *Oikos*, **111,** 437−444.

Tóth, J.P., Varga, K., Végvári, Z. & Varga, Z. (2013) Distribution of the Eastern knapweed fritillary (*Melitaea ornata* Cristoph, 1893) (Lepidoptera: Nymphalidae): past, present and future. *Journal of Insect Conservation*, **17,** 245–255.

Turchin, P., Wood, S.N., Ellner, S.P., Kendall, B.E., Murdoch, W.W., Fischlin, A., Casas, J., McCauley, E. & Biggs, C.J. (2003) Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology*, **84,** 1207−1214.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B*, **365,** 2025−2034.

Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, J.C., Kram, T., Krey, V., Lamarque, J-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J. & Rose, S.K. (2011) The representative concentration pathways: an overview. *Climatic Change*, **109,** 5–31.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, **220,** 589−594.

Vasconcelos, H.I. (1991) Mutualism between *Maieta guianensis* Aubl. a myrmecophytic melastome, and one of its ant inhabitants: ant protection against insect herbivores. *Oecologia*, **87,** 295−298.

Veldtman, R., McGeoch, M.A. & Scholtz, C.H. (2002) Variation in cocoon size in southern African wild silk moths: implications for sustainable harvesting. *African Entomology*, **10,** 127−136.

Veldtman, R., McGeoch, M.A. & Scholtz, C.H. (2004) Parasitoids of the southern African wild silk moths (Lepidoptera). *African Entomology*, **12,** 117−122.

Veldtman, R. (2005) The ecology of southern African wild silk moths (*Gonometa* species, Lepidoptera: Lasiocampidae): consequences for their sustainable use. PhD thesis, University of Pretoria, Pretoria, South Africa.

Veldtman, R., McGeoch, M.A. & Scholtz, C.H. (2007) Can life-history and defence traits predict the population dynamics and natural enemy responses of insect herbivores? *Ecological Entomology*, **32,** 662–673.

Wang, H.G., Marquis, R.J. & Baer, C.S. (2012) Both host plant and ecosystem engineer identity influence leaf-tie impacts on the arthropod community of *Quercus*. *Ecology*, **93,** 2186–2197.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414,** 65−69.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A. & Snyder, M.A. (2009) Niches, models, and climate change: Assessing the assumptions and uncertainties. *PNAS*, **106,** 19729–19736.

Wilby, A., Shachak, M. & Boeken, B. (2001) Integration of ecosystem engineering and trophic effects of herbivores. *Oikos*, **92,** 436–444.

Williams, D.W. & Liebhold, A.M. (2002) Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology*, **4,** 87–99.

Wisz, M.S., Hijmans, .J., Li, J., Peterson, A.T., Graham, C.H. and NCEAS Predicting Species Distributions Working Group. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14,** 763−773.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P. & Svenning, J-C. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88,** 15–30.

Witek, M., Nowicki, P., Śliwińska, E.B., Skórkam, P., Settele, J., Schönogge, K. & Woyiechowski, M. (2010) Local host ant specificity of *Phengaris* (*Maculinea*) *teleius* butterfly, an obligatory social parasite of *Myrmica* ants. *Ecological Entomology*, **35,** 557–564.

Worth, J.R.P., Williamson, G.J., Sakaguchi, S., Nevill, P.G. & Joran, G.J. (2014) Environmental niche modelling fails to predict Last Glacial Maximum refugia: niche shifts, microrefugia or incorrect palaeoclimate estimates? *Global Ecology and Biogeography*, **23,** 1186−1197.

Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41,** 496–506.

Wright, J.P. & Jones, C.G. (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations and challenges. *BioScience*, **56,** 203–209.

Young, T.P., Stubblefield, C.H. & Isbell, L.A. (1997) Ants on swollen thorn acacias: species coexistence in a simple system. *Oecologia*, **109,** 98–107.

Zhou, G., Baumgärtner, J. & Overholt, W.A. (2001) Impact assessment of an exotic parasitoid on stemborer (Lepidoptera) population dynamics in Kenya. *Ecological Applications*, **11,** 1554–1562.

Zurell, D., Jeltsch, F., Dormann, C.F. & Schröder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, **32,** 733−744.

APPENDIX A. Supplementary results from the models of *Gonometa* species host plant distributions.

The models predicting the current and future (2070) potential distributions of *G. postica* host plant species had a high predictive power, with test AUC values ranging from 0.72 to 0.87 (Table A1). A similar result was obtained for the models predicting the potential distributions of *G. rufobrunnea* host plants. These test AUC values ranged from 0.76 to 0.87. The good performance of the models is also reflected in the presence-absence maps generated for some of these species (Figs. B1−B6, Appendix B) – where it is apparent that the known occurrence localities of the species match their predicted distributions well. Variables that were important predictors of *Gonometa* host tree distributions are given in Table A2.

Table A1. Model performance for the predictions of the *Gonometa* host tree distributions which were predicted using climatic and soil data: *Burkea africana*, *Senegalia mellifera*, *Vachellia erioloba* and *V. tortilis* (*G. postica* hosts) and *Colophospermum mopane* and *Brachystegia spicifomis* (*G. rufobrunnea* hosts). The AUC is the area under the curve and is used as a measure of model performance. SD = standard deviation and gain = a likelihood statistic (maximising the probability of host plant presence in relation to background data) for the test data (i.e. data used to evaluate how well Maxent predicts independent data)

Model	Test AUC	Training AUC	SD AUC	Test gain
B. africana	0.8312	0.8844	0.018	0.7564
S. mellifera	0.772	0.8231	0.0233	0.5567
V. erioloba	0.8731	0.9012	0.0122	1.081
V. tortilis	0.727	0.7887	0.0213	0.3381
C. mopane	0.8713	0.9097	0.0125	1.0202
B. spiciformis	0.7606	0.9268	0.0469	0.0841

Table A2. Variables that were found to be the important (i.e. variables contributing most to the models and which yielded the highest training gain and AUC scores based on the jackknife tests of variable importance) for describing the *Gonometa* spp. host tree distributions. Variables marked with asterisks did not contribute highly to the models based the analysis of variable contribution, but were important predictors of moth distribution based on the jackknife tests of variable importance. Permutation importance is determined by randomly permuting values of the variable in question among the training points. The gain given in the table starts at 0 during a model run, increasing towards an asymptote and gives the maximum likelihood ratios of average presences to average background points (see Merow *et al*., 2013). Maximizing the gain gives the best models. The training gain without the variable represents the model gain once the variable in question has been removed from the model, whereas the training gain with the variable only, represents the gain of the model when the variable in question is considered in isolation from all the other variables. The AUC (without variable) represents predictive power of the models when the variables in question are excluded from the models, and the AUC (variable only) represents AUC from a model containing only the predictor variable

Model	Variable	% Contribution	Permutation importance	Training gain (without variable)	Training gain (variable only)	AUC (without variable)	AUC (variable only)
B. africana	Mean Temperature of the Driest Quarter	25.5681	35.1369	0.8899	0.3211	0.8291	0.7139
	Annual Precipitation	23.2019	15.3021	0.8668	0.3337	0.8243	0.7105
	Precipitation Seasonality	27.7642	34.9022	0.8863	0.4072	0.8195	0.7355
S. mellifera	Annual Precipitation	38.6518	18.2594	0.5475	0.2945	0.7642	0.7115
	Precipitation Seasonality	17.787	21.5	0.5127	0.1973	0.7627	0.6626
	soil pH*	4.8394	0.6776	0.5657	0.2111	0.7683	0.7045
V. erioloba	Mean Temperature of the Driest Quarter	23.9543	9.7546	1.1439	0.5921	0.8727	0.7977
	Annual Precipitation	36.5267	7.5442	1.1234	0.6527	0.8716	0.7786
	Precipitation of the Driest Quarter	17.1367	30.7425	1.126	0.3811	0.8713	0.7032
	% Sand*	7.3755	13.8438	1.13	0.4332	0.8701	0.7791
V. tortilis	Annual Precipitation	48.1459	35.0566	0.3948	0.2631	0.7114	0.6521
	Precipitation of the Coldest Quarter	15.0712	11.6579	0.4541	0.1676	0.7213	0.6069
	soil pH*	3.0124	3.6015	0.4571	0.15	0.7263	0.6518
C. mopane	Mean Temperature of the Driest Quarter	23.2135	31.4052	1.1167	0.5686	0.8609	0.7662
	Annual Precipitation	20.0928	12.8124	1.1633	0.3556	0.8601	0.7094
	Precipitation Seasonality	31.6771	36.5521	1.1479	0.5891	0.8616	0.7708
	Precipitation Coldest Quarter	10.1203	2.226	1.2024	0.5365	0.8736	0.7458
B. spiciformis	Annual Mean Temperature	0.8147	3.73	1.274	0.1506	0.7582	0.7144
	Annual Precipitation	41.3221	16.2732	1.2051	0.514	0.7501	0.7695
	Soil pH*	2.3323	3.7594	1.2613	0.4675	0.7622	0.7532

APPENDIX B. Presence-absence maps generated for *Gonometa postica* and *Gonometa rufobrunnea* host plants for the current climate and under future climate change.

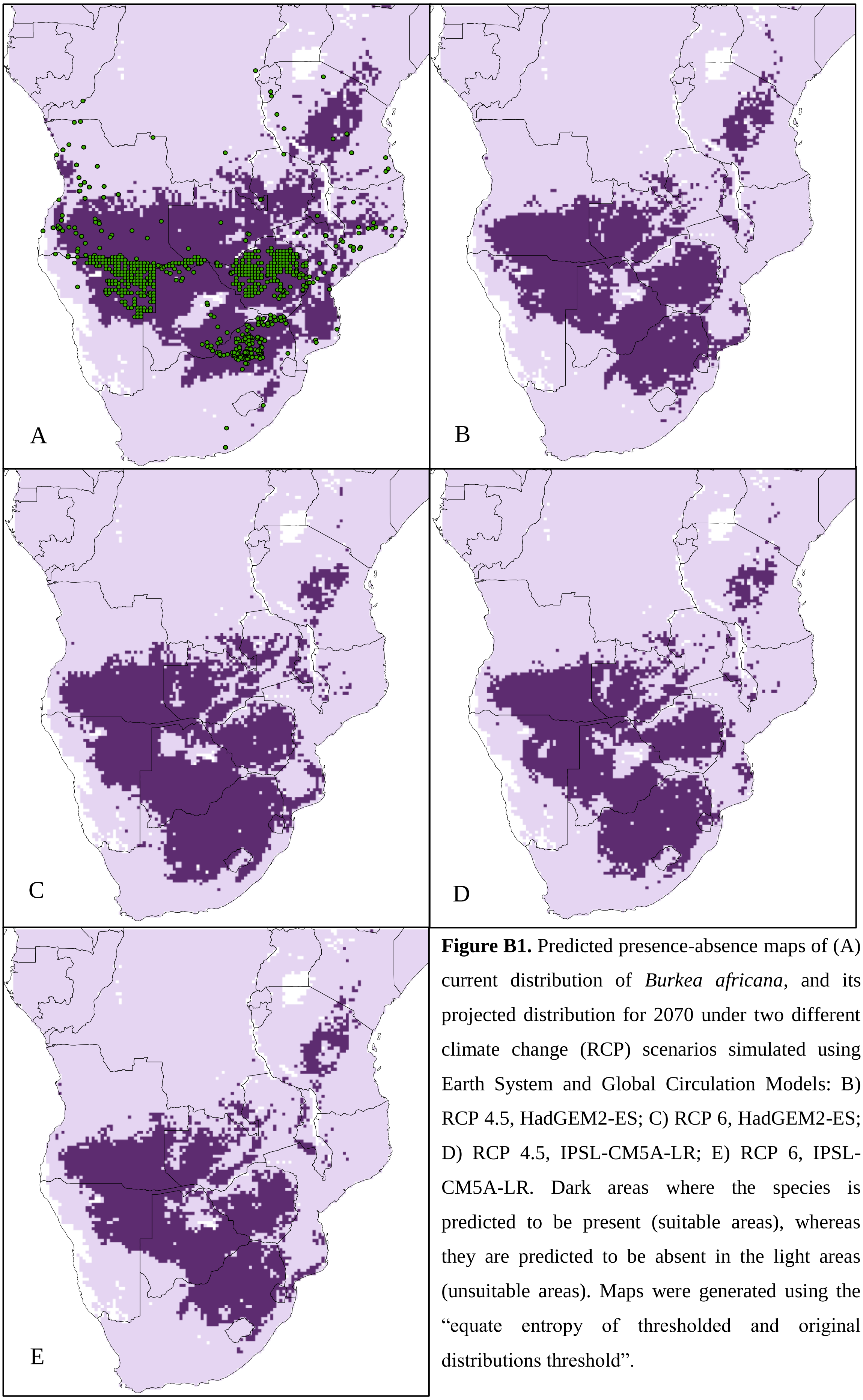


Figure B1. Predicted presence-absence maps of (A) current distribution of *Burkea africana*, and its projected distribution for 2070 under two different climate change (RCP) scenarios simulated using Earth System and Global Circulation Models: B) RCP 4.5, HadGEM2-ES; C) RCP 6, HadGEM2-ES; D) RCP 4.5, IPSL-CM5A-LR; E) RCP 6, IPSL-CM5A-LR. Dark areas where the species is predicted to be present (suitable areas), whereas they are predicted to be absent in the light areas (unsuitable areas). Maps were generated using the “equate entropy of thresholded and original distributions threshold”.

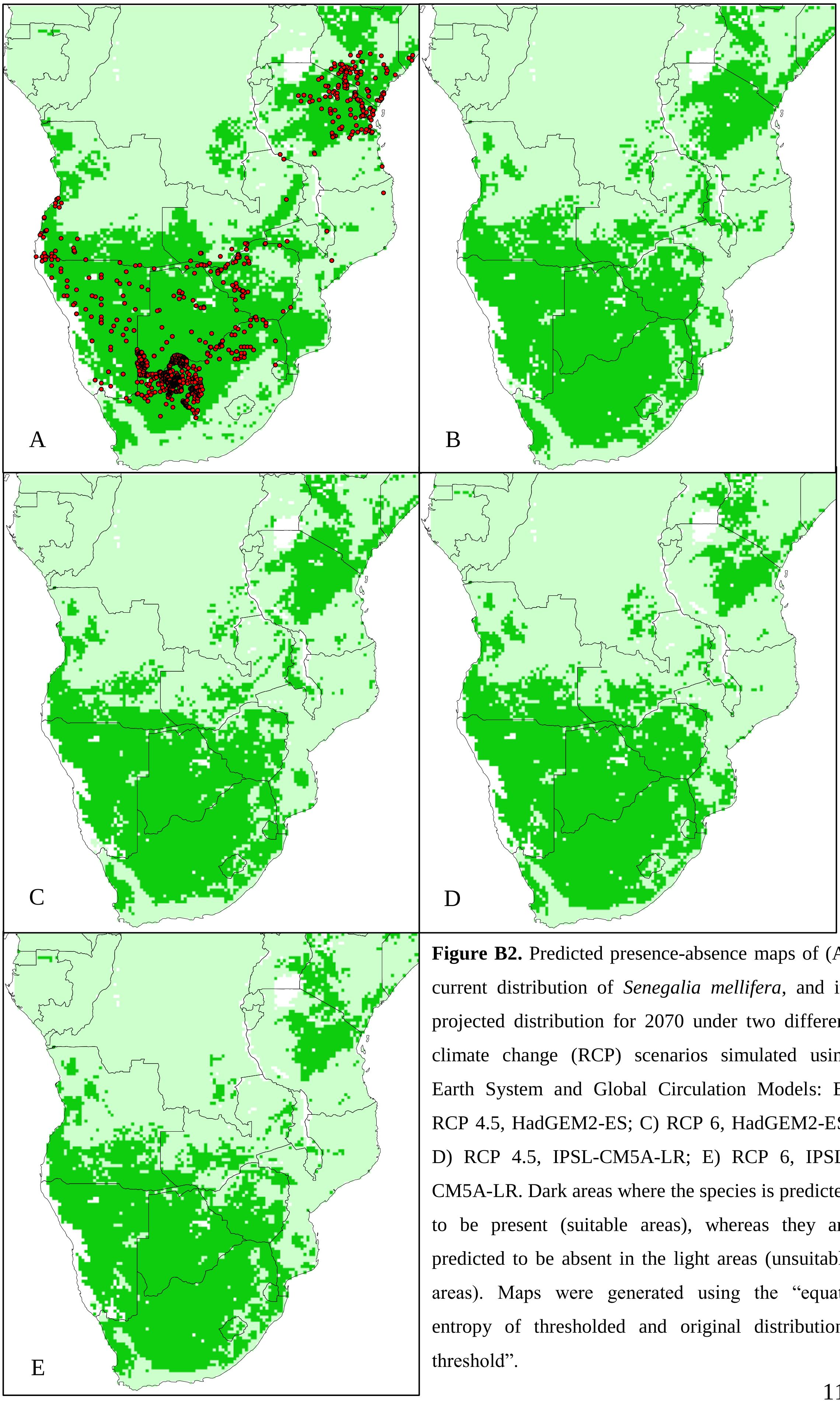
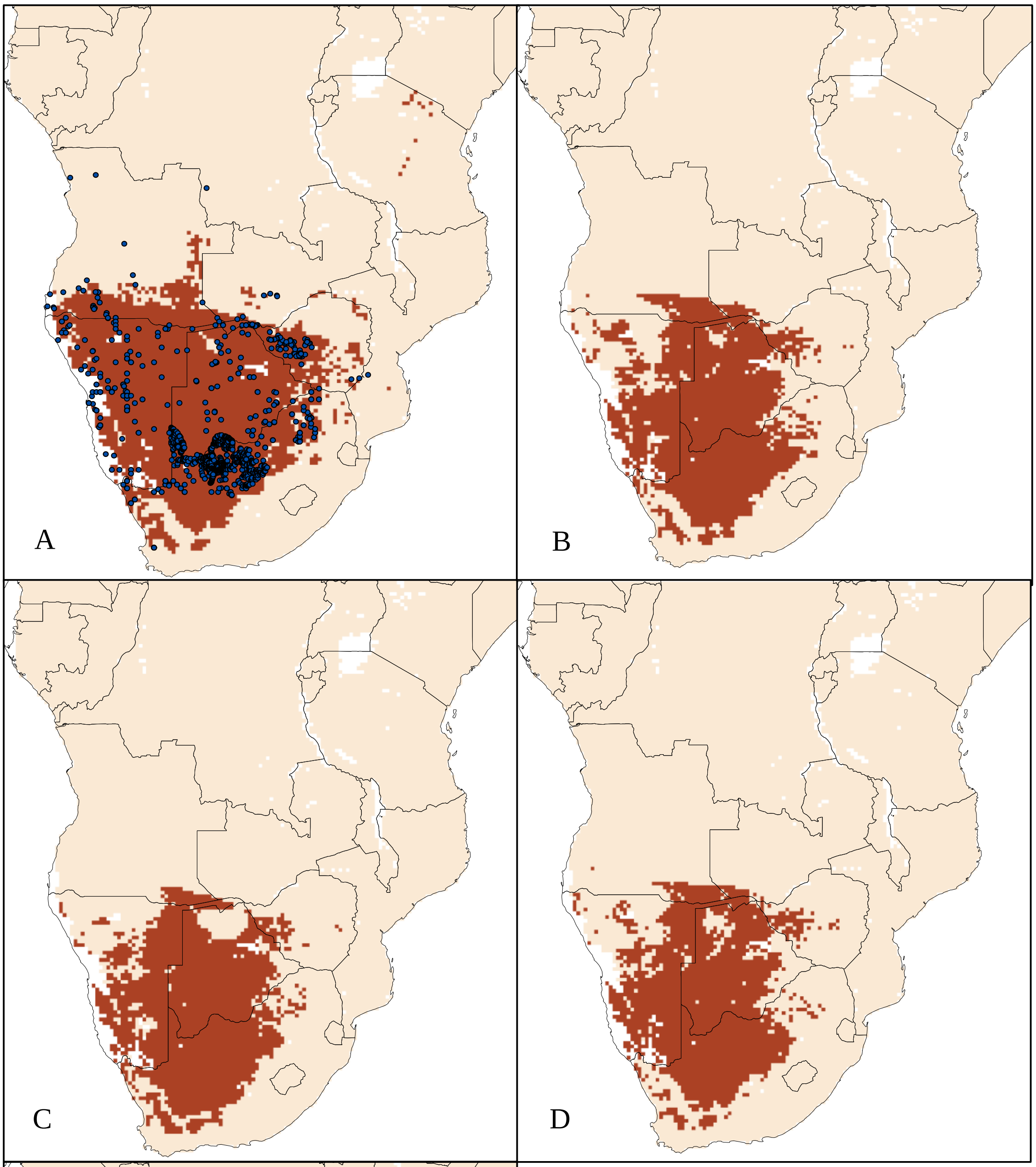


Figure B2. Predicted presence-absence maps of (A) current distribution of *Senegalia mellifera*, and its projected distribution for 2070 under two different climate change (RCP) scenarios simulated using Earth System and Global Circulation Models: B) RCP 4.5, HadGEM2-ES; C) RCP 6, HadGEM2-ES; D) RCP 4.5, IPSL-CM5A-LR; E) RCP 6, IPSL-CM5A-LR. Dark areas where the species is predicted to be present (suitable areas), whereas they are predicted to be absent in the light areas (unsuitable areas). Maps were generated using the “equate entropy of thresholded and original distributions threshold”.



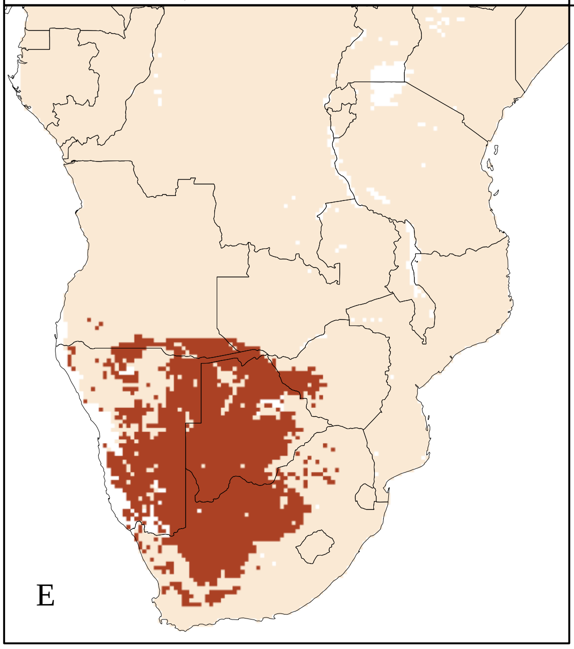


Figure B3. Predicted presence-absence maps of (A) current distribution of *Vachellia erioloba*, and its projected distribution for 2070 under two different climate change (RCP) scenarios simulated using Earth System and Global Circulation Models: B) RCP 4.5, HadGEM2-ES; C) RCP 6, HadGEM2-ES; D) RCP 4.5, IPSL-CM5A-LR; E) RCP 6, IPSL-CM5A-LR. Dark areas where the species is predicted to be present (suitable areas), whereas they are predicted to be absent in the light areas (unsuitable areas). Maps were generated using the "equate entropy of thresholded and original distributions threshold".

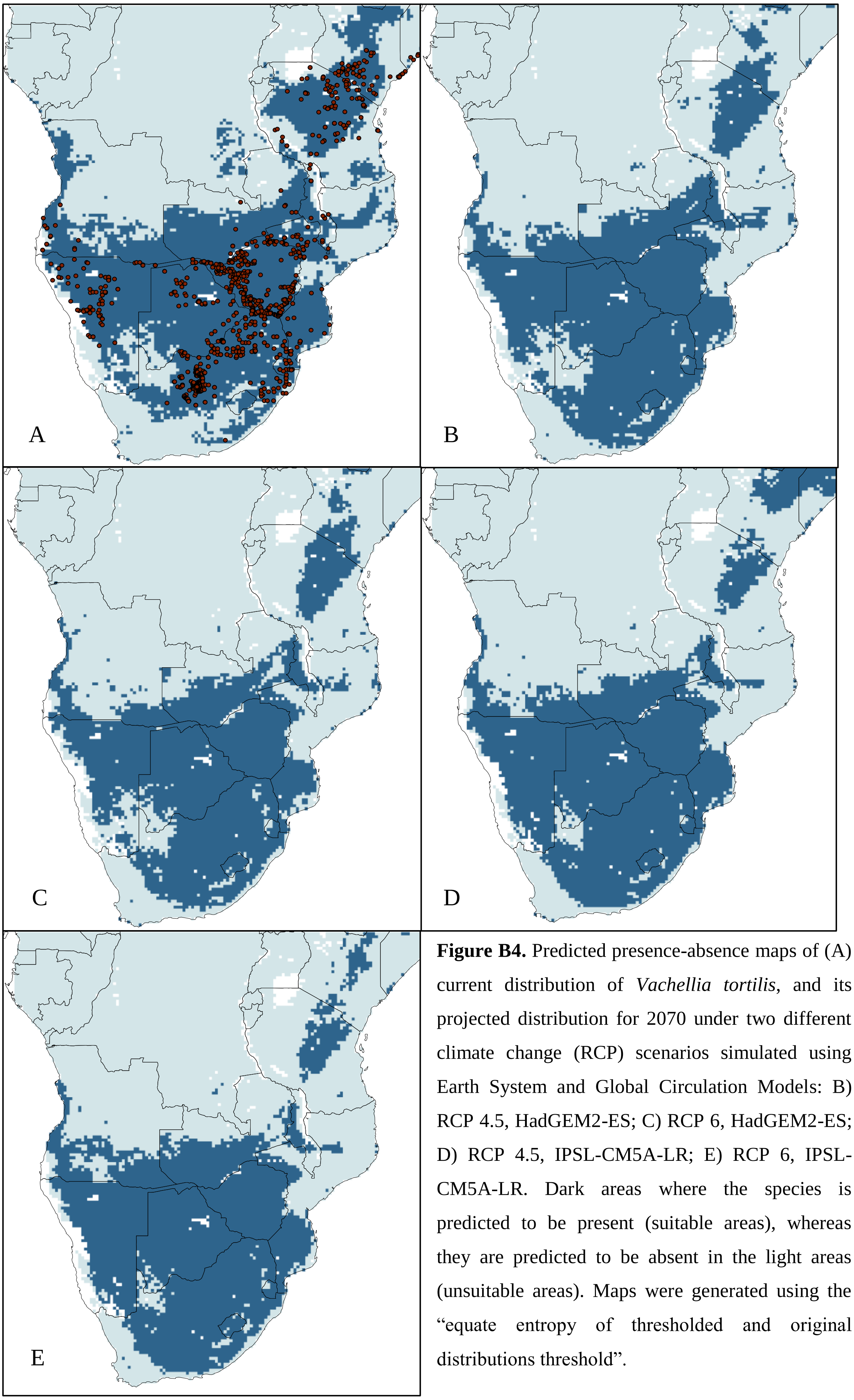


Figure B4. Predicted presence-absence maps of (A) current distribution of *Vachellia tortilis*, and its projected distribution for 2070 under two different climate change (RCP) scenarios simulated using Earth System and Global Circulation Models: B) RCP 4.5, HadGEM2-ES; C) RCP 6, HadGEM2-ES; D) RCP 4.5, IPSL-CM5A-LR; E) RCP 6, IPSL-CM5A-LR. Dark areas where the species is predicted to be present (suitable areas), whereas they are predicted to be absent in the light areas (unsuitable areas). Maps were generated using the "equate entropy of thresholded and original distributions threshold".

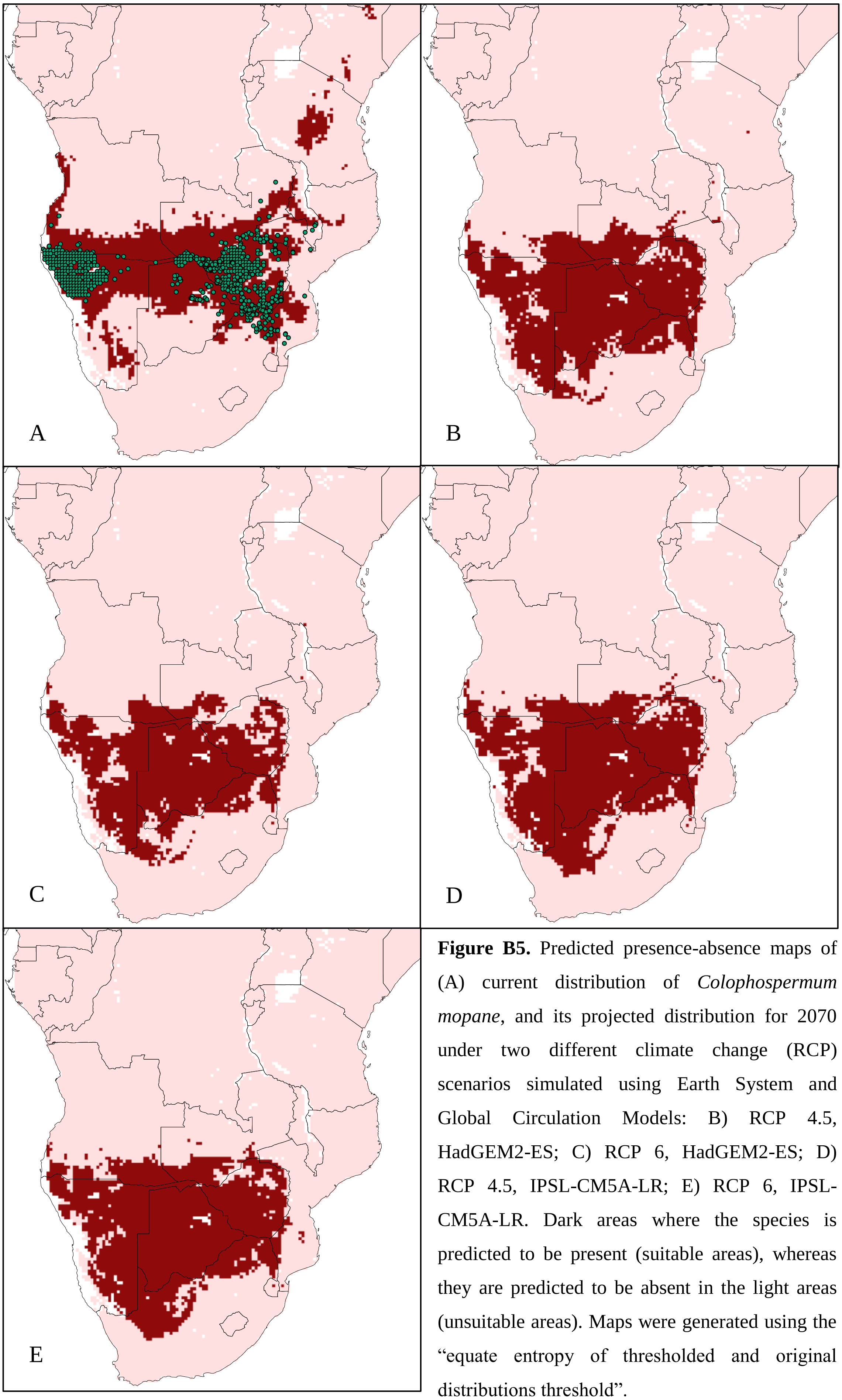


Figure B5. Predicted presence-absence maps of (A) current distribution of *Colophospermum mopane*, and its projected distribution for 2070 under two different climate change (RCP) scenarios simulated using Earth System and Global Circulation Models: B) RCP 4.5, HadGEM2-ES; C) RCP 6, HadGEM2-ES; D) RCP 4.5, IPSL-CM5A-LR; E) RCP 6, IPSL-CM5A-LR. Dark areas where the species is predicted to be present (suitable areas), whereas they are predicted to be absent in the light areas (unsuitable areas). Maps were generated using the "equate entropy of thresholded and original distributions threshold".

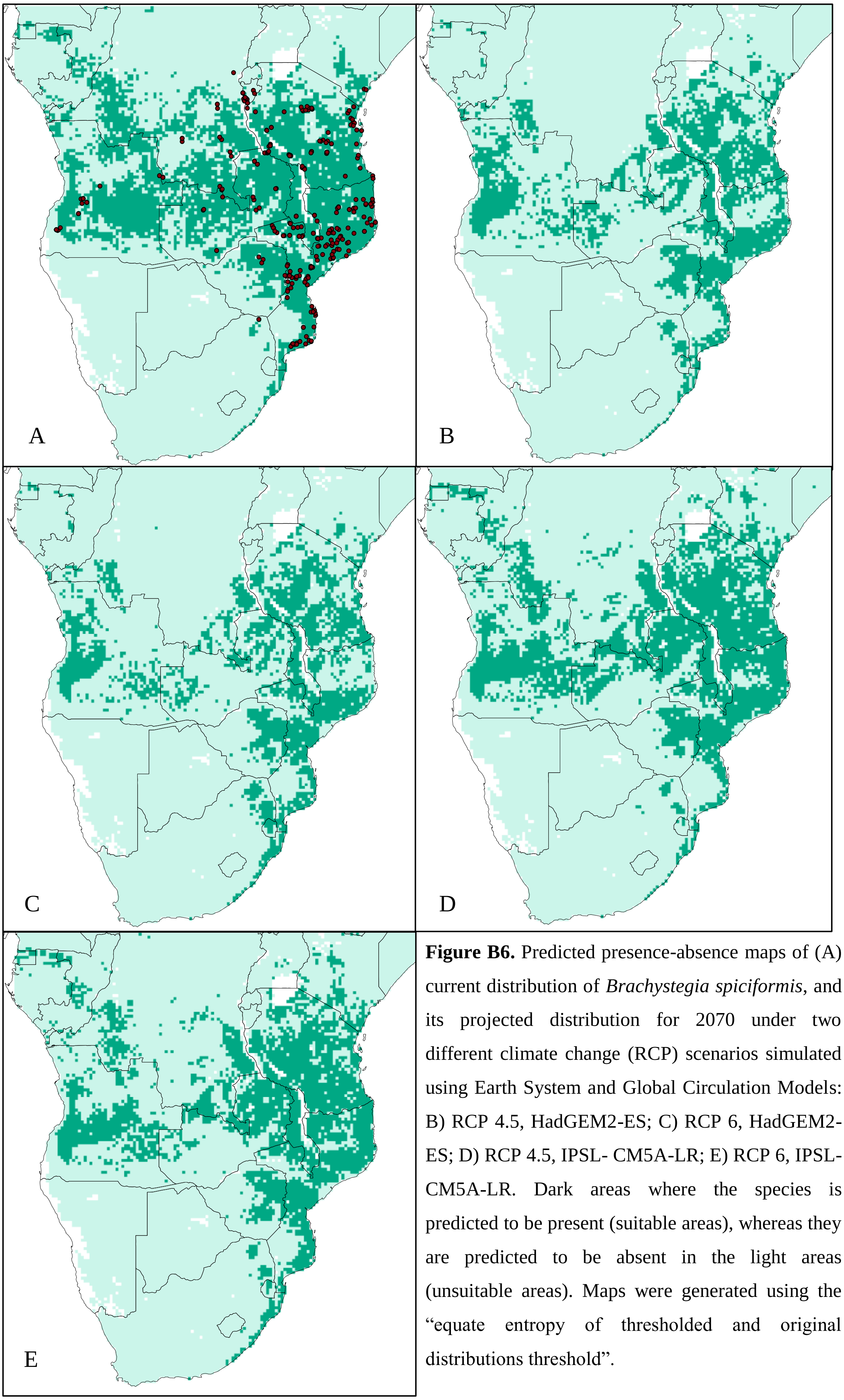


Figure B6. Predicted presence-absence maps of (A) current distribution of *Brachystegia spiciformis*, and its projected distribution for 2070 under two different climate change (RCP) scenarios simulated using Earth System and Global Circulation Models: B) RCP 4.5, HadGEM2-ES; C) RCP 6, HadGEM2-ES; D) RCP 4.5, IPSL- CM5A-LR; E) RCP 6, IPSL-CM5A-LR. Dark areas where the species is predicted to be present (suitable areas), whereas they are predicted to be absent in the light areas (unsuitable areas). Maps were generated using the "equate entropy of thresholded and original distributions threshold".

APPENDIX C. Response curves for abiotic and biotic *Gonometa postica* and *Gonometa rufobrunnea* SDMs. Figures illustrate how the probability of occurrence of the *Gonometa* species varied with the environmental predictor variables that were used for modelling.

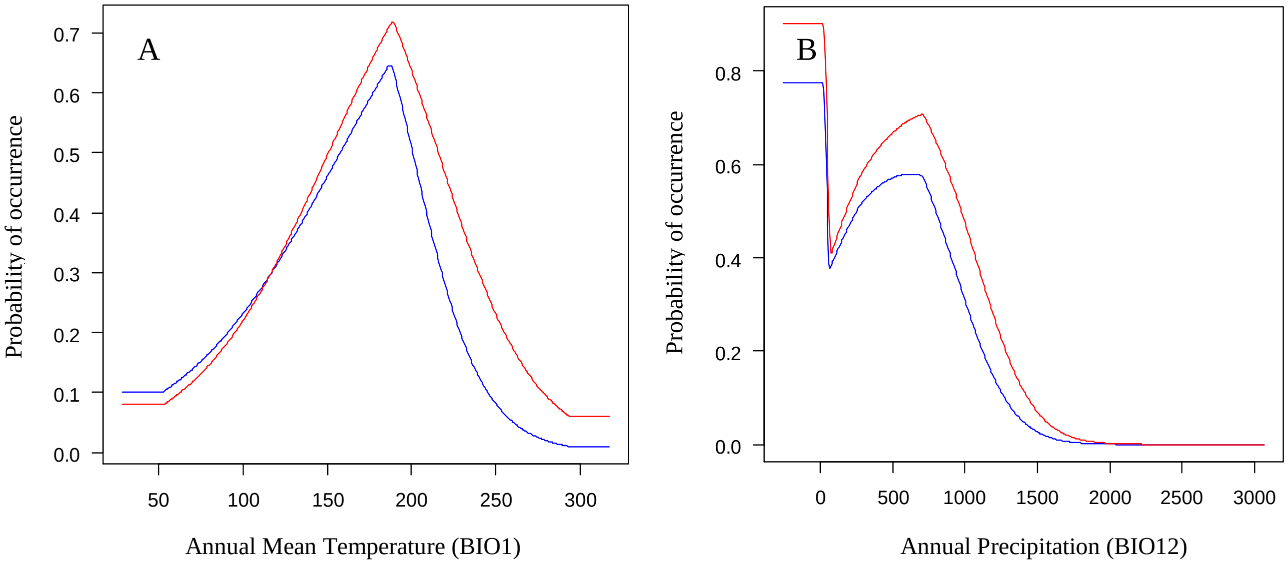


Figure C1. Response curves of important predictor variables for the abiotic model of *Gonometa postica* distribution. The lines show how the probability of occurrence of *G. postica* changes with each predictor variable: A) Annual Mean Temperature and B) Annual Precipitation. Blue lines represent species occurrence when the variable in question is considered independently from the other predictor variables. The red lines consider each variable's effect on the species occurrence whilst accounting for the effects of all other predictor variables.

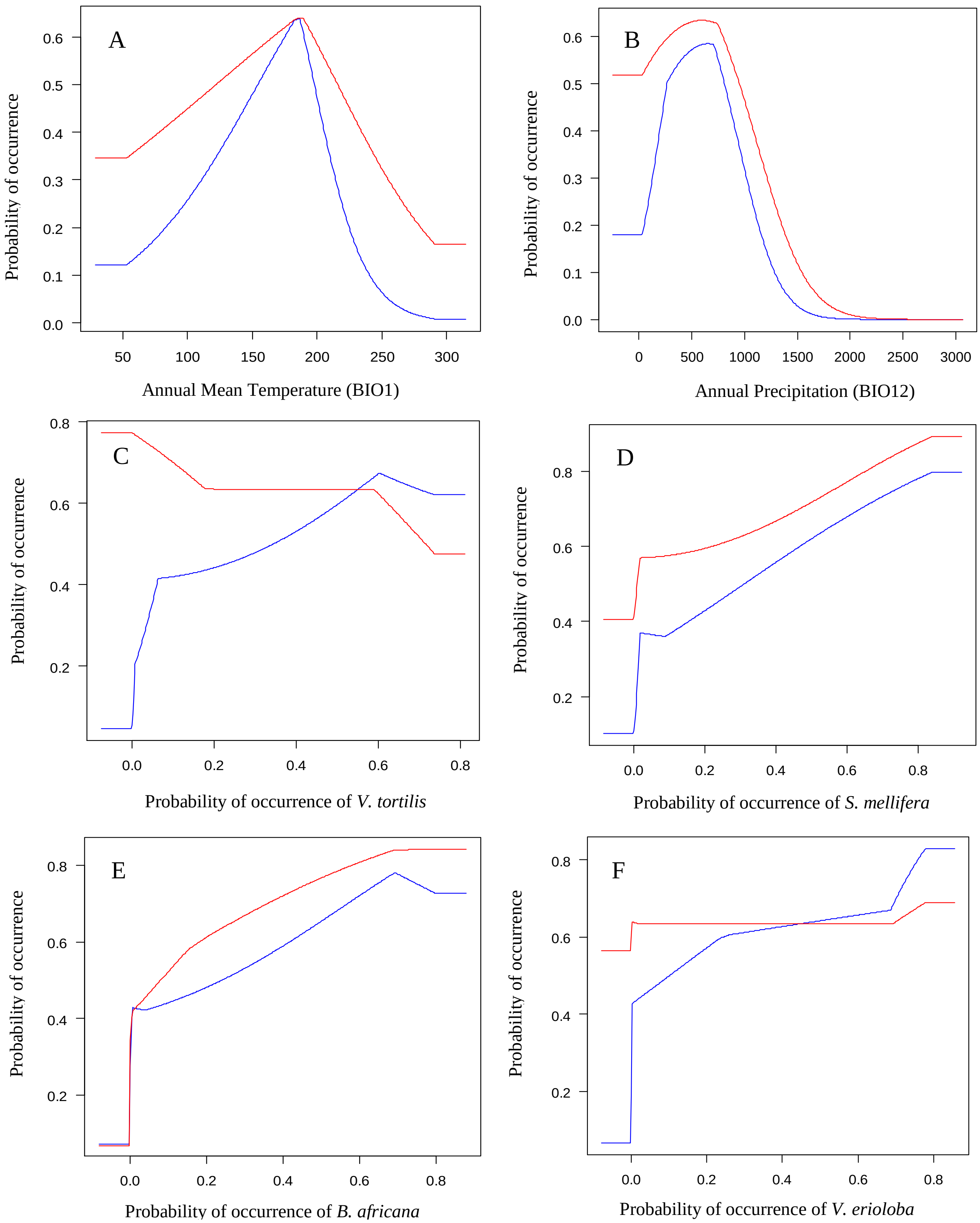


Figure C2. Response curves for important predictor variables of *Gonometa postica* distribution for Biotic model 1. The lines show how the probability of occurrence of *G. postica* changes with each predictor variable: A) Annual Mean Temperature, B) Annual Precipitation, C) *V. tortilis*, D) *S. mellifera* occurrence, E) *B. africana* occurrence and F) *V. erioloba*. Blue lines represent species occurrence when the variable in question is considered independently from the other predictor variables. The red lines consider each variable's effect on the species occurrence whilst accounting for the effects of all other predictor variables.

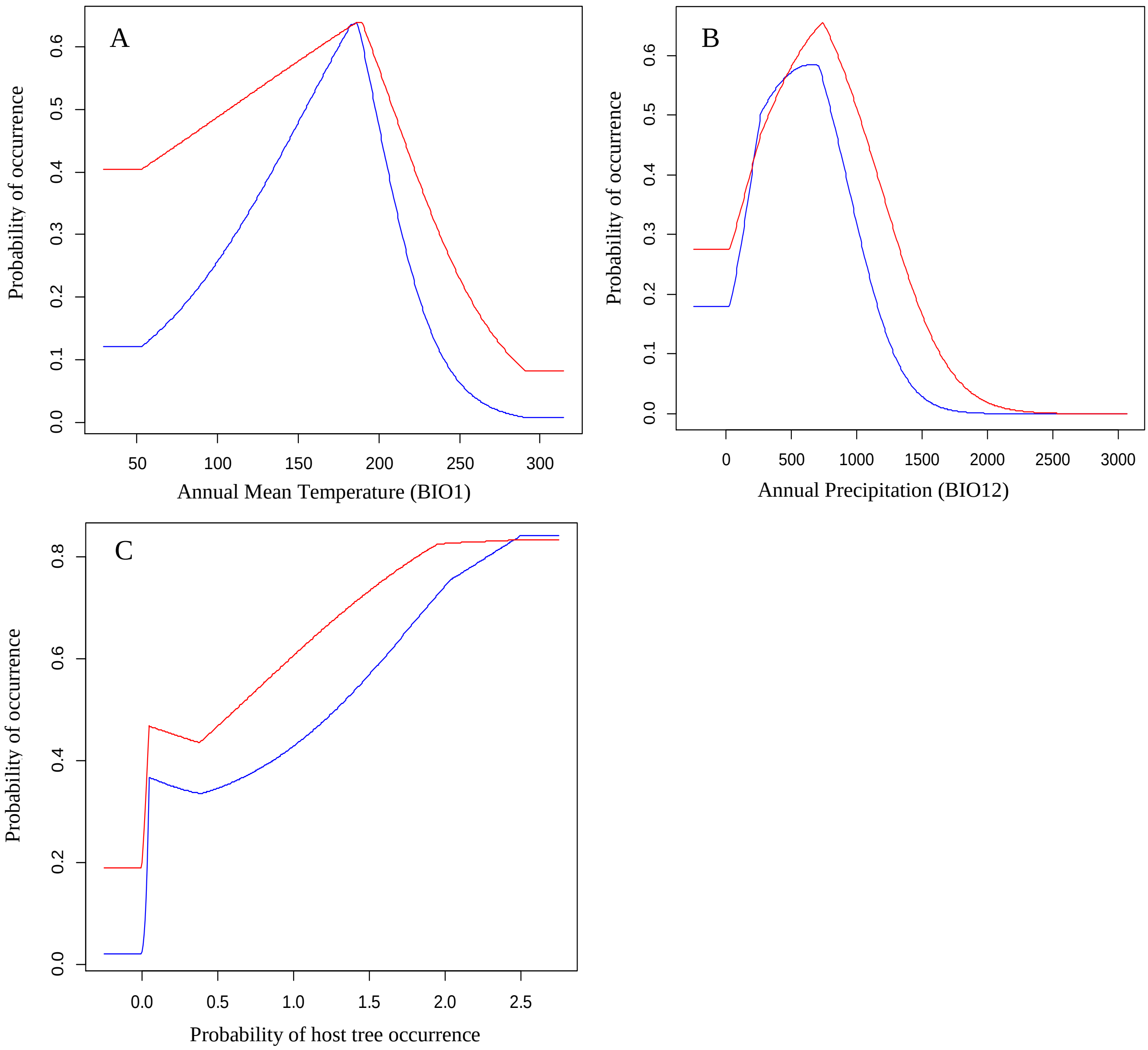


Figure C3. Response curves for important predictor variables of *Gonometa postica* distribution for Biotic model 4. The lines show how the probability of occurrence of *G. postica* changes with each predictor variable: A) Annual Mean Temperature, B) Annual Precipitation and C) Host plant distribution. Blue lines represent species occurrence when the variable in question is considered independently from the other predictor variables. The red lines consider each variable's effect on the species occurrence whilst accounting for the effects of all other predictor variables.

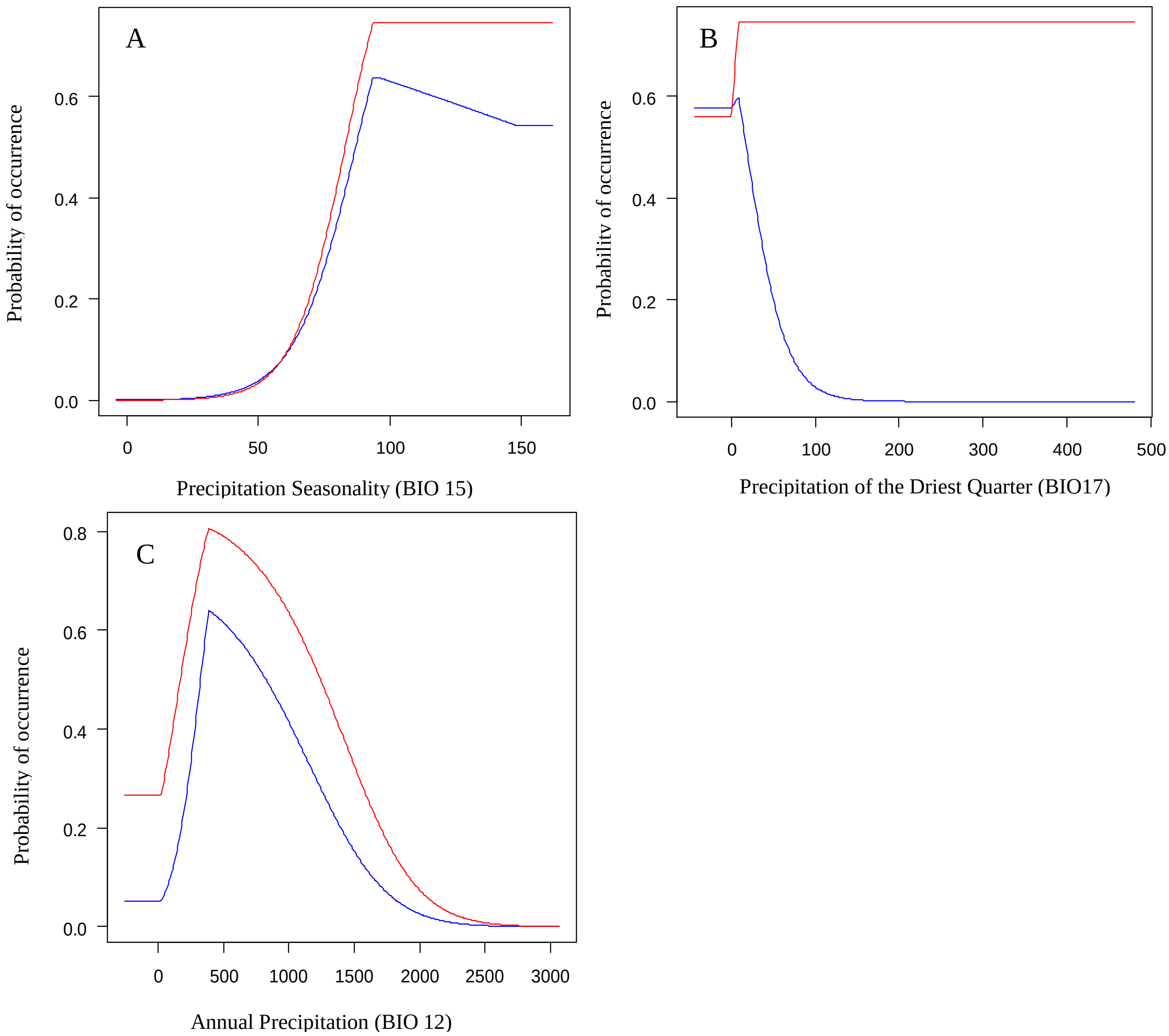


Figure C4. Response curves for important predictor variables of *Gonometa rufobrunnea* distribution for the Abiotic model. The lines show how the probability of occurrence of *G. rufobrunnea* changes with each predictor variable: A) Precipitation Seasonality, B) Precipitation of the Driest Quarter and C) Annual Precipitation. Blue lines represent species occurrence when the variable in question is considered independently from the other predictor variables. The red lines consider each variable's effect on the species occurrence whilst accounting for the effects of all other predictor variables.

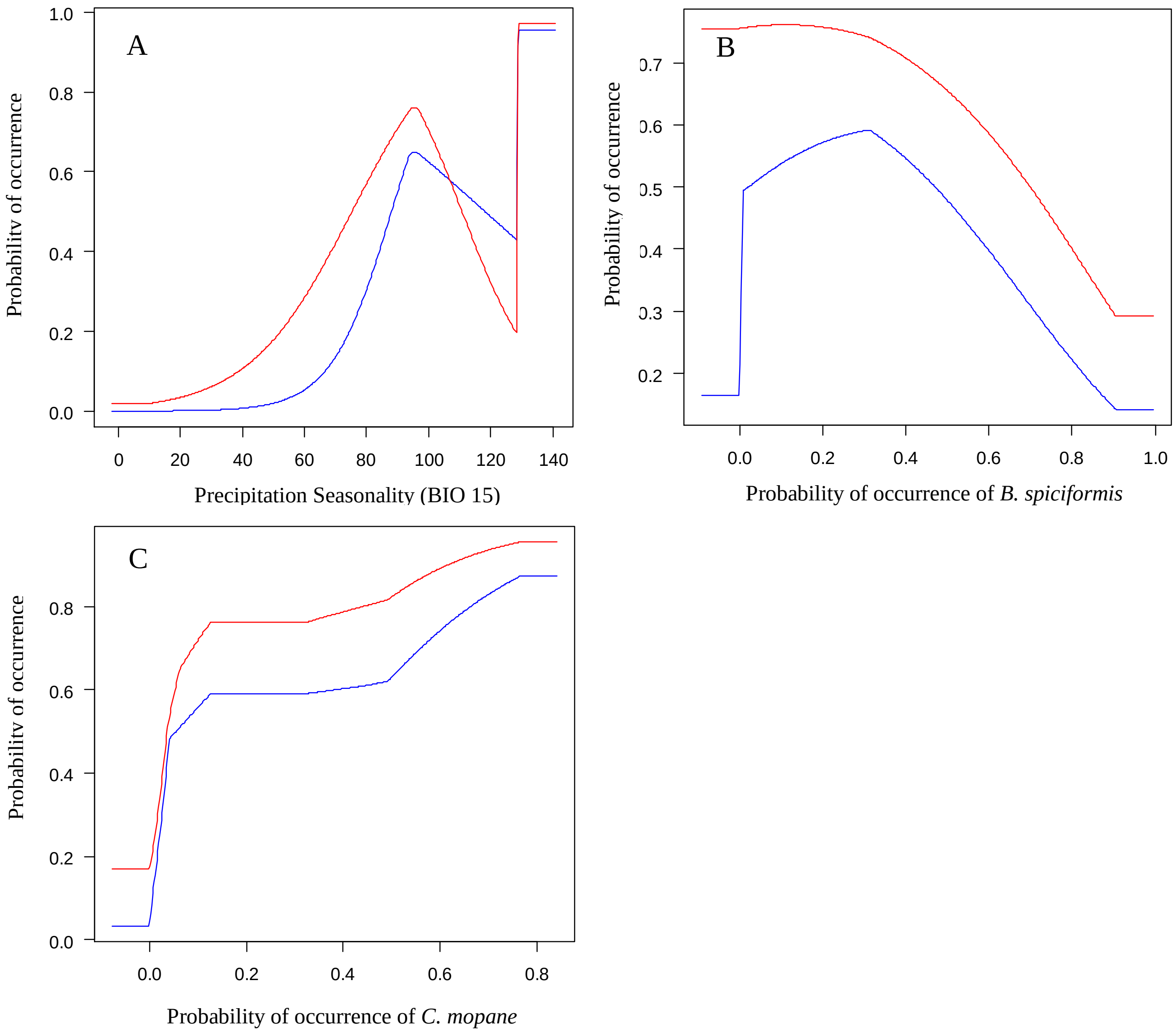


Figure C5. Response curves for important predictor variables of *Gonometa rufobrunnea* distribution for Biotic 1. The lines show how the probability of occurrence of *G. rufobrunnea* changes with each predictor variable: A) Precipitation Seasonality, B) Occurrence probability of *B. spiciformis* and C) Occurrence probability of *C. mopane* varies when considered independently from the other predictor variables. Blue lines represent species occurrence when the variable in question is considered independently from the other predictor variables. The red lines consider each variable's effect on the species occurrence whilst accounting for the effects of all other predictor variables.

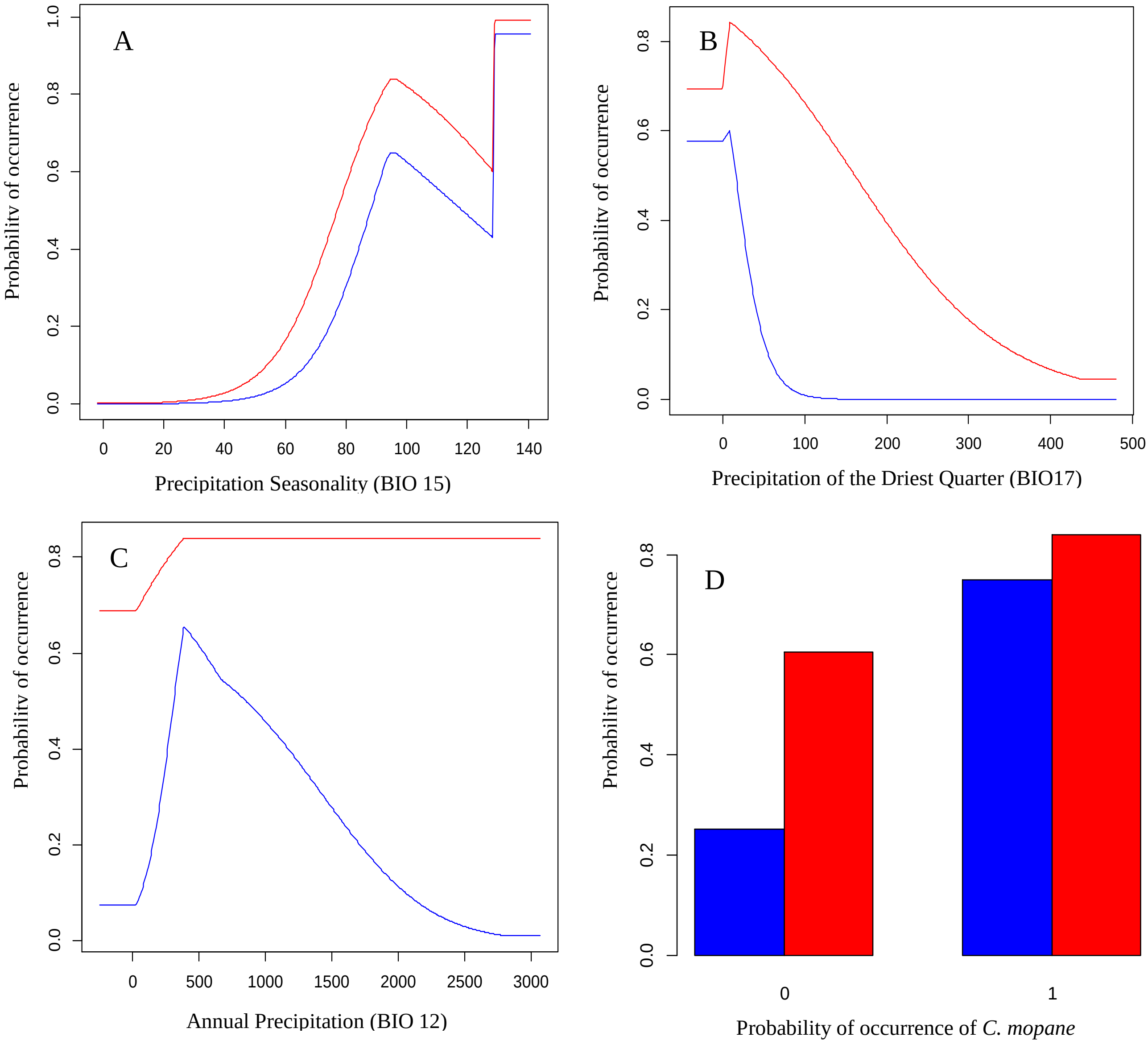


Figure C6. Response curves for important predictor variables of *Gonometa rufobrunnea* distribution for Biotic 2. The lines show how the probability of occurrence of *G. rufobrunnea* changes with each predictor variable: A) Precipitation Seasonality, B) Precipitation of the Driest Quarter, C) Annual Precipitation, and D) Occurrence probability of *C. mopane* varies when considered independently from the other predictor variables. Blue lines represent species occurrence when the variable in question is considered independently from the other predictor variables. The red lines consider each variable's effect on the species occurrence whilst accounting for the effects of all other predictor variables.

APPENDIX D. The ecological significance of *Gonometa postica:* a habitat creator for ants and other invertebrates on *Vachellia erioloba*

Table D1. Results from the minimum adequate mixed effect hurdle model testing the effects of cocoon characteristics on (A) ant abundance (n = 102 cocoons, n = 35 trees, $p < 0.05$) and (B) ant presence-absence (n = 287 cocoons, n = 50 trees, $p < 0.05$). Two additional predictor variables (i.e. distances of cocoons from the tree trunk and the number of holes present in the cocoons) were considered in this analysis; however, these predictors were not included in the minimum adequate models. Abbreviations: P = cocoons containing one or more small parasite holes; E = emerged cocoons and ES = emerged cocoons with secondary holes; Pr = other invertebrates present and Ab = other invertebrates absent

A. *Fixed effects*	Level	Estimate	SE	z value	p-value
(Intercept)	-	2.357	0.610	3.860	**< 0.001**
Width	-	0.069	0.033	2.090	**0.037**
Hole type	P > ES = E	-	-	-	**0.012**
Other invertebrates	Pr > Ab	-	-	-	**0.016**

B. *Fixed effects*	Level	Estimate	SE	z value	p-value
(Intercept)	-	-1.967	1.068	-1.840	**0.066**
Hole type	P > ES > E	-	-	-	**< 0.001**
Other invertebrates	Pr > Ab	-	-	-	**< 0.001**
Length	-	0.073	0.030	2.430	**0.015**
Random effect	SD	Variance			
(1|Tree)	0.917	0.841			

Table D2. Results from a minimum adequate mixed effect model testing the effects of cocoon characteristics on *Crematogaster* sp. 1 abundance (n = 270 cocoons, $p < 0.05$). Abbreviations: P = cocoons containing one or more small parasite holes; E = emerged cocoons and ES = emerged cocoons with secondary holes; Pr = other invertebrates present and Ab = other invertebrates absent

Variable	Level	Estimate	SE	z-value	p-value
(Intercept)	-	2.434	0.376	6.47	**< 0.001**
Width	-	0.097	0.019	5.09	**< 0.001**
Hole type	P = ES = E, P > E	-	-	-	**0.005**
Time of day	-	-0.016	0.01	-1.62	0.105
Other invertebrates	Pr > Ab	-	-	-	**< 0.001**
Random effect	SD	Variance			
(1|Tree)	0.222	0.471			