



Faculty of Resource Science and Technology

**Diversity and Spatial Distribution of Scarabaeidae (Insecta: Coleoptera)
in Sarawak**

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Diversity and Spatial Distribution of Scarabaeidae (Insecta: Coleoptera) in Sarawak

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DECLARATION

I declare that the work in this thesis was carried out in accordance with the regulations of Universiti Malaysia Sarawak. Except where due acknowledgements have been made, the work is that of the author alone. The thesis has not been accepted for any degree and is not concurrently submitted in candidature of any other degree.



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ABSTRACT

Beetles of Scarabaeidae have many ecological roles in terrestrial ecosystems. They are important as agricultural pests, biological control agents, pollinators, decomposers, and biological and environmental indicators. Despite their abundance in the ecosystem, there is no comprehensive checklist of scarab beetle, and lack of distribution models of the studied taxa to map high biodiversity area using their distribution. Hence, this study aims to document and compare the diversity of scarab beetles and predict their spatial distribution across different localities in Sarawak. Therefore, this study utilised various sampling methods such as handpicking, aerial netting, baited traps, flight intercept traps, and light traps covering 17 localities within Sarawak. As a result, a total of 1,551 beetle individuals were collected representing 126 total species from six subfamilies (Apodiinae, Cetoniinae, Dynastinae, Melolonthinae, Rutelinae, and Scarabaeinae). Among these, Melolonthinae was recorded as the most speciose and abundant subfamily with 49 species (39.99%) and 909 individuals (58.61%), respectively. In terms of individual count, the most abundant species was represented by *Apogonia destructor* with 315 individuals (20.31%). By localities, Sebangkoi is the most speciose site recorded with 46 beetle species, whereas Samunsam Wildlife Sanctuary was recorded with the most abundant with 311 individuals. Overall, Sabal Agroforestry had the highest biodiversity indices (Simpson 1-D = 0.9451; Shannon = 3.352). Besides, heath forest was recorded as the most diverse forest type for scarab beetles (Simpson 1-D = 0.9655; Shannon = 3.548). Additionally, the Jaccard similarity index was calculated between localities and forest types, where Gua Temurang and Gua Raya were found to have the highest index among all localities with 0.381. Meanwhile, limestone forests and mixed dipterocarp forests shared the highest Jaccard similarity index of 0.2609. For spatial distribution of Scarabaeidae in Sarawak, selected genera, namely, *Ixorida* sp.

(AUC = 85.4%), *Chalcosoma* spp. (AUC = 85.1%), *Apogonia* spp. (AUC = 90.6%), *Anomala* spp. (AUC = 90.1%) and *Onthophagus* spp. (AUC = 87.0%) were analysed and all models showed similar distribution prediction toward the coastal line of Sarawak. Of these, Bio 4, Bio 13, Bio 15, Bio 17, and Bio 18 were found as the most contributing environmental variables, representing temperature seasonality, precipitation of wettest month, precipitation seasonality, precipitation of driest quarter and precipitation of warmest quarter, respectively. In general, these models could be useful especially to the local authorities for future planning of biodiversity conservation and ecosystem's management. However, it is recommended that further studies can be rigorously conducted in terrestrial landscapes to provide a more comprehensive database for future conservation efforts.

Keywords: Diversity, ecology, spatial distribution models, Scarab beetles, Sarawak

Kepelbagaian dan Taburan Ruang Kumbang Scarab (Insecta: Coleoptera) di Sarawak

ABSTRAK

Kumbang daripada famili Scarabaeidae mempunyai banyak fungsi ekologi dalam ekosistem daratan. Kumbang-kumbang ini penting sebagai serangga perosak tanaman, agen kawalan biologi, pendebunga, pengurai, serta penunjuk biologi dan alam sekitar. Walaupun kumbang-kumbang ini banyak ditemui dalam ekosistem, tiada senarai komprehensif yang tersedia untuk kumbang Scarab, dan tiada model yang dibangunkan untuk memetakan kawasan yang mempunyai biodiversiti tinggi menggunakan taburan kumbang. Oleh itu, kajian ini dijalankan untuk mendokumentasi dan membandingkan kepelbagaian kumbang Scarab serta meramalkan taburan ruang kumbang di pelbagai lokasi di Sarawak. Justeru, kajian ini menggunakan pelbagai kaedah penyampelan seperti kutipan, jaring udara, perangkap berumpan, perangkap pintasan penerbangan, dan perangkap cahaya yang merangkumi 17 lokasi di Sarawak. Sejumlah 1,551 individu kumbang telah dikumpulkan yang mewakili 126 spesies daripada enam subfamili (Apodiinae, Cetoniinae, Dynastinae, Melolonthinae, Rutelinae dan Scarabaeinae). Antara subfamili ini, Melolonthinae direkodkan sebagai subfamili yang paling banyak spesies dan individu iaitu 49 spesies (39.99%) dan 909 individu (58.61%), masing-masing. Dari segi bilangan individu, Apogonia destructor mempunyai bilangan tertinggi iaitu 315 individu (20.31%). Dari segi lokasi, Sebangkoi merupakan lokasi yang mempunyai spesies terbanyak dengan 46 spesies kumbang, manakala Sanktuari Hidupan Liar Samunsam merekodkan bilangan individu tertinggi dengan 311 individu. Secara keseluruhan, Sabal Agroforestry mempunyai indeks biodiversiti tertinggi (Simpson 1-D = 0.9451; Shannon = 3.352). Selain itu, hutan kerangas direkodkan sebagai jenis hutan yang paling digemari oleh kumbang Scarab (Simpson 1-D = 0.9655; Shannon = 3.548). Selain itu, pengiraan indeks persamaan Jaccard juga dibuat

antara lokasi dan jenis hutan, yang mana Gua Temurang dan Gua Raya mempunyai indeks tertinggi di antara semua lokasi iaitu 0.381, manakala hutan batu kapur dan hutan dipterokarpa campuran mempunyai indeks persamaan Jaccard tertinggi yang sama iaitu 0.2609. Bagi taburan ruang Scarabaeidae di Sarawak, genera tertentu iaitu Ixorida sp. (AUC = 85.4%), Chalcosoma spp. (AUC = 85.1%), Apogonia spp. (AUC = 90.6%), Anomala spp. (AUC = 90.1%) dan Onthophagus spp. (AUC = 87.0%) dianalisis dan semua model menunjukkan ramalan taburan yang serupa iaitu menjurus ke arah garis pantai Sarawak. Daripada ini, Bio 4, Bio 13, Bio 15, Bio 17, dan Bio 18 didapati sebagai pembolehubah alam sekitar yang paling signifikan, masing-masing mewakili kebolehubahan suhu, hujan pada bulan paling basah, kebolehubahan hujan, hujan pada suku paling kering dan hujan pada suku paling panas. Secara umumnya, model ini berguna terutamanya kepada pihak berkuasa tempatan untuk perancangan pemuliharaan biodiversiti dan pengurusan ekosistem pada masa hadapan. Walau bagaimanapun, adalah disyorkan bahawa kajian lanjut boleh dijalankan secara lebih terperinci merangkumi landskap daratan untuk menyediakan pangkalan data yang komprehensif untuk usaha pemuliharaan masa hadapan.

Kata kunci: Kepelbagaian, ekologi, model pengedaran keruangan, kumbang Scarab, Sarawak

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LIST OF ABBREVIATIONS

MPLT	Modified Pennsylvanian light trap
GGNP	Gunung Gading National Park
RLL	Real Living Lab
KSL	Kampung Serpan Laut
ABR	Adis Buan Resort
MS	Mount Serumbu
SA	Sabal Agroforestry
GN	Gunung Ngelik
Smt	Sematan
Sbk	Sebangkoi
LBNP	Loagan Bunut National Park
LHNP	Lambir Hills National Park
SWS	Samunsam Wildlife Sanctuary
GT	Gua Temurang
FC	Fairy Cave
Gp	Gumpey
GR	Gua Raya
NNP	Niah National Park
HF	Heath forest
LsF	Limestone forest
LtF	Littoral forest
MF	Mangrove forest

MDF	Mixed dipterocarp forest
PSF	Peat swamp forest
PAST	Paleontological Statistics Software Package
SDM	Spatial Distribution Model
GIS	Geographic Information System
QGIS	Quantum Geographic Information System
mm	millimetre
m	metre
ROC	Receiver operating curve
AUC	Area under the curve

CHAPTER 1

INTRODUCTION

1.1 Introduction

Scarab beetles are a diverse group of insects belonging to the family Scarabaeidae, which is part of the order Coleoptera. They are often recognised by their distinctive shape, with either oval or elongated clubbed antennae. Scarab beetles can vary greatly in size, ranging from a few millimetres to several centimetres in length. These beetles are found worldwide, inhabiting many habitats, including forests, grasslands, deserts, and even urban areas as they have developed various feeding guilds (Erwin & Geraci, 2009). One of the most famous scarab beetles is the sacred scarab (*Scarabaeus sacer*) of ancient Egypt, which was revered as a symbol of resurrection and transformation (Ward, 1994). Although most of the Scarabaeidae members are not recorded in Red List of Threatened Species in International Union for Conservation of Nature (IUCN) due to lack of assessment, some species like *Thorectes* and *Synapsis* are listed.

Scarab beetles play various roles in their ecosystems. Many species are scavengers, feeding on decaying organic matter such as dung, dead animals, and rotting vegetation. Others are herbivores, consuming plant material or roots. Some members are even considered pests in agriculture, damaging crops or causing economic losses since the grubs feed on the roots while the adults feed on the exposed parts of plants (Jackson & Klein, 2006). For example, *Oryctes rhinoceros*, a type of Dynastinae that has serious impact on oil palm plantations (Manjeri et al., 2014) In addition to their ecological importance, scarab beetles have cultural significance in many societies. They have been depicted in art,

mythology, and religion for thousands of years, often symbolising concepts like rebirth, fertility, or protection (Ratcliffe, 2006). One notable behaviour of scarab beetles is their habit of rolling balls of dung, which they use for food or as a brood chamber for their eggs. This behaviour has fascinated scientists and observers for centuries and has been the subject of much study.

Beetles possess a complex public image; a species can be either a pest or a conservation target according to the place or the change of status over time (New, 2010). According to Bodo et al. (2021), deforestation, urbanisation, anthropogenic activities, along with other human activities pollute or destroy natural habitats. Although these activities are important in the aspects of economy and development, they are also causing many other consequences to environment and cause habitat loss for wild flora and fauna species. Despite the fact that some restrictions and preventions were executed by the government and the authorities to ensure minimum loss, the efforts to implement sustainable development should encompass the element of wildlife conservation in ensuring a healthy biodiversity. Wildlife conservation, also known as the protection of nature habitat areas of flora and fauna to prevent overexploitation and human activity damage, is one of the most discussed topics and most significant challenges faced by communities and conservationists globally (Convention on Biological Diversity, 2010).

In our daily lives, necessities like air, water, food, shelter, and clothing are provided by our ecosystem. To ensure that our ecosystem is healthy and sufficient for all, a balance of biodiversity is essential because all processes supporting living organisms around the globe rely on a wide range of microorganisms, plants, and animals. Therefore, a diversity checklist is essential for conservationists to plan or propose any conservation plan in the

future. As part of the ecosystem, the value of beetles as bioindicators has been proclaimed by many workers, surrogate wider biodiversity in responding to changes in any environment (New, 2010), especially for Scarabaeidae which is highly reliant on the environmental conditions throughout their whole life cycle.

1.2 Problem Statement

Insufficient data has always been a limitation to the effectiveness of planning and implementation of conservation actions in highly diverse tropical ecosystems, particularly remote areas. Whittaker et al. (2005) categorised the scarcity of information into two key elements, termed the ‘Linnaean’ and ‘Wallacean’ shortfalls. The Linnaean shortfall refers to the limited knowledge of how many and what kind of species exist. On the other hand, Wallacean shortfall refers to insufficient information regarding the status and population of particular species. Hence in this study, the scarab beetles in Sarawak falls under the Linnaean shortfall category, of which there is no comprehensive documentation of beetles have been published.

The declination of Scarabaeidae diversity is an alert of loss in biodiversity health, since there are many important roles played by Scarabaeidae in the ecosystem even our human society. As example, dung beetles are one of the best decomposers that help in nutrient cycle, but they are also indicating the risk of diversity loss when loss in population number. Then, scarab beetles also have members who pollinate plants instead of bees (Sakai and Inoue, 1999). *Cyclocephala alata* (Scarabaeidae, Dynastinae) is a good example of Scarabaeidae as an exclusive pollinator for *Philodendron acutatum*, an Araceae (Maia et al, 2010). Unfortunately, the insufficient species checklist of Scarabaeidae in Sarawak remains an obstacle to contributing to the conservation of biodiversity until now. Additionally, there

is also a lack of a distribution model to map high-diversity area using Scarabaeidae distribution records in Sarawak.

1.3 Objectives

The objectives of this research were:

- i. To compare the assemblages and diversity of Scarabaeidae from 17 sites with different forest types across Sarawak.
- ii. To predict the spatial distribution of Scarabaeidae in Sarawak.

First, this research presented a preliminary checklist of Scarabaeidae in Sarawak to update the database and convenience for further conservation planning or pre-development surveys. Comparisons among the assemblages and diversity of Scarabaeidae from different localities and forest types were conducted to provide a better overview of the interaction between Scarabaeidae and their physical environment. Other than that, the Scarabaeidae diversity study also indirectly provides an overview of biodiversity health to conservationists or researchers.

Besides Scarabaeidae diversity, the mapping of spatial distribution for Scarabaeidae was also conducted in this research. With the aid of spatial distribution modelings on genera of Scarabaeidae, the predictions of Scarabaeidae dispersal according to genus were provided with a wider vision helping the study of the dynamic shift of scarab beetles across Sarawak along localities with different environmental conditions.

1.4 Chapter Summary

This thesis is separated into six chapters, starting with an introduction, followed by a comprehensive review of the literatures and the general methodology. In the fourth chapter, the analysis of Scarabaeidae diversity in Sarawak was conducted, while the spatial

distribution of Scarabaeidae in Sarawak was discussed in Chapter 5. Lastly, a general summary and conclusion were included as Chapter 6 before list of references and appendices.

CHAPTER 2

LITERATURE REVIEW

2.1 Background of Scarabaeidae

2.1.1 Overview

Scarabaeidae (Latreille, 1802), a beetle family classified under the superfamily Scarabaeoidea and order Coleoptera has 33,504 species globally (Ghosh et al., 2020). The Coleoptera name came from an old Greek word “koleos” meaning sheath and wings stand for “ptera” (NC State University, 2015). Scarabaeidae was classified under the suborder Polyphaga with undivided visible first sternite by coxa (Figure 2.1) (Choate, 1999). Traces of Scarabaeidae can be tracked in cultures or mythology from Egypt until nowadays especially the behaviour of dung rolling. (Ratcliffe, 2006). Scarabaeidae was known to have several subfamilies such as Cetoniinae (flower chafers), Dynastinae (rhinoceros beetles), Melolonthinae (June beetles), Rutelinae (shinning leaf chafers), Scarabaeinae (dung beetles) and others.

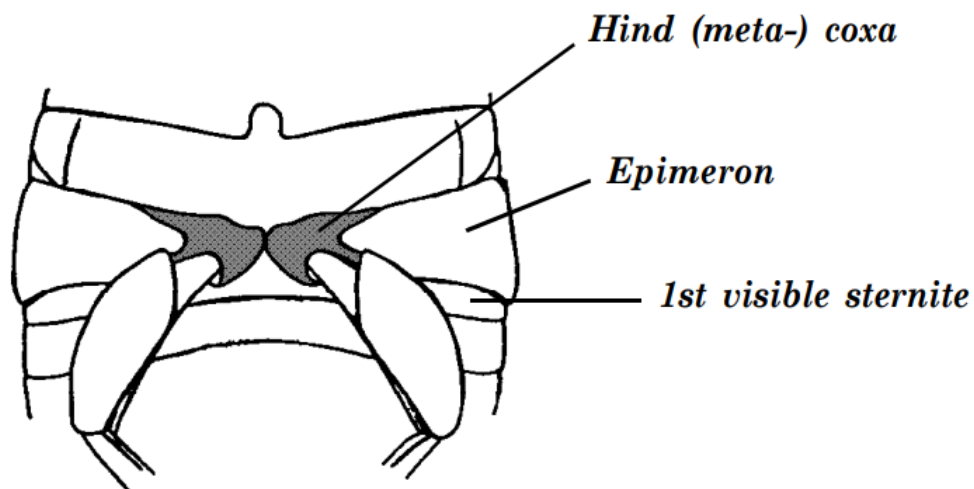


Figure 2.1: The first visible sternite of the Polyphaga suborder is not divided by hindcoxa (adapted from Choate, 1999)

2.1.2 Biology of Scarabaeidae

Scarabaeidae mostly have a one to two-year life cycle with four stages of life, from grubs to adult individuals (Wylie & Speight, 2012). Normally after mating occurs nearby their feeding area like oil palm trees or trees containing more tree sap, the female will lay eggs beneath the ground substrate which is slightly acidic and has lower humidity. The grubs of Scarabaeidae spend their three larva instars before metamorphosis underground, filter-feeding rotten plants, organic structures from the dirt, or even roots of grasses. At the same time, adults like Cetoniinae, Dynastinae, Rutelinae, Melolonthinae are strictly phytophagous which leads to various types of habitat like mixed dipterocarp forest, littoral forest, limestone forest and others (Figure 2.2) (Malcolm, 2015). Gill (2001) stated that although most of Scarabaeinae, the real dung beetle was known for their dung feeding behaviour in both larva and adult stages, of which carrions, mushrooms, rotting fruits, and decomposing plant materials are also preferred food for certain species of Scarabaeinae (Ritcher, 1958; Triplehorn et al., 2005; Frank, 2017).

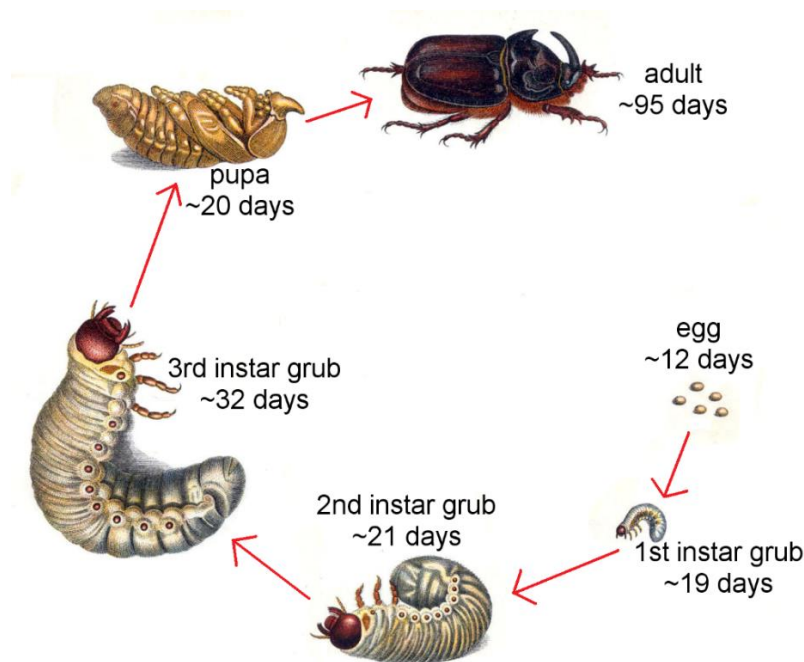


Figure 2.2: Life cycle of a rhinoceros beetle (adapted from Malcolm, 2015)

2.1.3 Characteristics of Scarabaeidae (Latreille, 1802)

Having three-segmented bodies, three pairs of legs, and two pairs of wings classified scarab beetles from other invertebrates. They are also known as endopterygotes as complete metamorphosis occurs in them (Kristensen, 1999). Like other coleopterans, Scarabaeidae's adults have membranous hind wings and are covered by hardened forewings with lesser veins called elytra (Bouchard, 2004), which evolved to protect and contribute to body support. Triangular or parabolic-shaped scutellum often can be found on Scarabaeidae (Ratchliffe & Jameson, 2001). Their unique features, which set them apart from other beetle families, included a C-shaped body posture (Figure 2.3) that is rugose and hairy in the larval stage, 8–11 segmented antennae with lamellate ends (Figure 2.4) (Reid & Bulbert, 2016), a visible head from above, robust bodies, and spikes on their five segmented tarsi (5–5–5) (Figure 2.5) in the adult stage (NC State University, 2015).



Figure 2.3: Scarabaeidae grub with C-shaped posture (Illionis Public Media, 2023)



Figure 2.4: Scarabaeidae antennae with lamellae ends

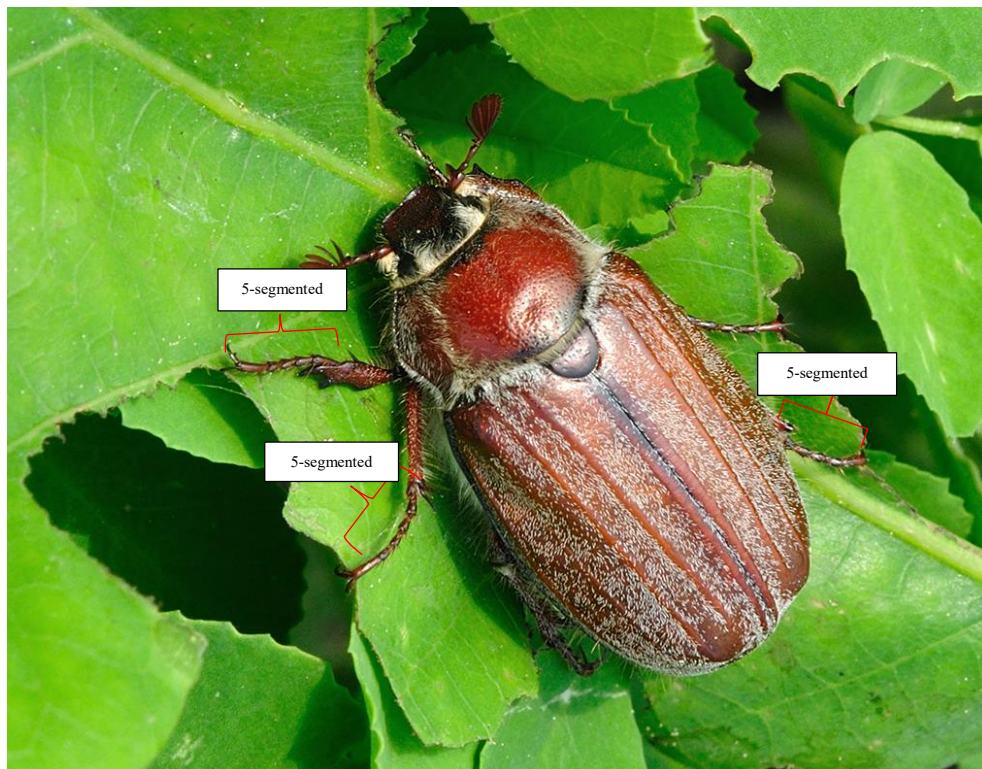


Figure 2.5: Scarabaeidae with five segmented tarsi (5-5-5) (Illionis Public Media, 2023)

2.1.3.1 Characteristics of Cetoniinae (Leach, 1815)

Cetoniinae are mostly known as flower chafers as they accumulate around blossoming trees with a bright and often metallic appearance. Cetoniinae has 10 segmented antennae with visible antennae bases on the above. Emarginated elytra without narrow membranous margins also allow them to have quick take off with closed elytra (Figure 2.6) (Reid & Bulbert, 2016). Besides that, large scutellum is often found in Cetoniinae (Hill & Abang, 2010; Reid & Bulbert, 2016).

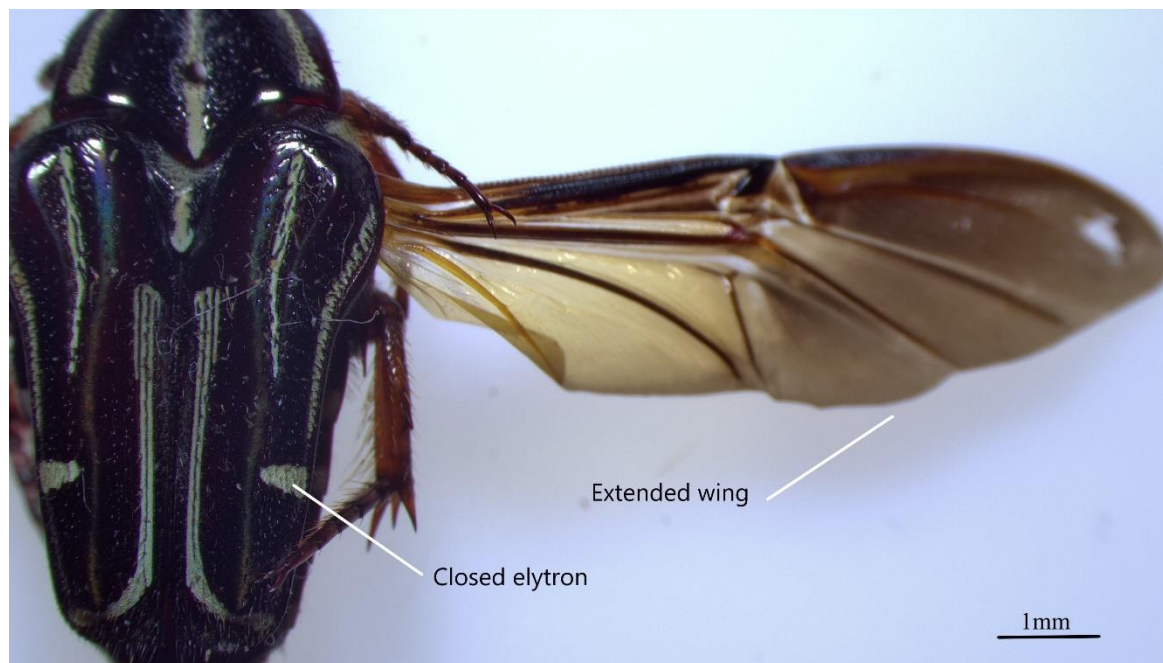


Figure 2.6: Cetoniinae extending the wing with enclosed elytron

2.1.3.2 Characteristics of Dynastinae (MacLeay, 1819)

Rhinoceros beetles, a species of Dynastinae, are herbivorous beetles with horn-like protuberances on male adults' heads or, in some cases, pronotums (Figures 2.7 & 2.8) which are purposed in fighting over mate rights, food sources in trees, logs, and even crops except for Phileurini, certain Cyclocephalini, and Pentodonini. Sometimes the male Dynastinae also classified into two groups, macro and micro due to the length and size of their horns which

are highly affected by the food sources that can be found within the environment. Not only do the protuberances differ in sex, but so does the dimorphism in the morphology of the final sternite, emarginated in male adults while round in female adults. Exposed mandibles from various degrees in dorsal view, nine or ten segmented antennae, equaled width for pronotum base and elytra with exposed pygidium (Figure 2.7), and visible scutellum are several key components to identify Dynastinae. Aside from some Cetoniinae and Carabidae species, most Dynastinae species are among the world's largest beetle species. Adult Dynastinae are known as Herculean beetles because of their incredible strength. Some adult species can move things 30-100 times their own weight (Ratcliffe et al., 2021).



Figure 2.7: Dynastinae with protuberances on head and pronotum, elytra with same width as pronotum base



Figure 2.8: Dynastinae female (left) and male (right) adults

2.1.3.3 Characteristics of Melolonthinae (MacLeay, 1819)

According to Evans (2001), Melolonthinae are one of the largest subfamilies in Scarabaeidae having broadly oval and convex bodies, normally known as May beetles, June beetles, or chafers. Their enlarged clypeus covering mouthparts (Figure 2.9) with lamellated mandibles and clearly setose and scaly elytra (Figure 2.10) with exposed scutellum or dorsal view distinguish them. In terms of antennae, the majority of Melolonthinae have seven to 10 segmented antennae with concealed antennae bases from above and three to seven elongated lamellae which are similar to a fan. Additionally, to differ between Melolonthinae and Rutelinae, their tarsal claws are the key component for identification since the tarsal claws on every Rutelinae leg can be moved independently unlike Melolonthinae.



Figure 2.9: Melolonthinae with clypeus covering mouthparts



Figure 2.10: Melolonthinae with setose and scaly elytra

2.1.3.4 Characteristics of Rutelinae (MacLeay, 1819)

Rutelinae, also known as Shinning Leaf chafers, are closely related to Melolonthinae in appearance, except for their antennae, tarsal claw, elytra, and others. In comparison to Melolonthinae, most Rutelinae have nine or ten segments of antennae with three segmented lamellae club, bright and metallic elytra with membranous edges (Figure 2.11). Rutelinae

are medium-sized beetles that range in colour from brilliant bright to drab brown or grey. Rutelinae are distinguished by their proportionally small antennae and huge yet somewhat convex eyes. Male Rutelinae mostly have extended elytra and narrower than females' in the aspect of sexual dimorphism (Jameson, 2001).



Figure 2.11: Rutelinae with bright or metallic elytra

2.1.3.5 Characteristics of Scarabaeinae (Latreille, 1802)

According to Gill (2001), Scarabaeinae has expanded clypeus which covers their mouthpart with lamelliform and membranous mandibles. Eight or nine-segmented antennae with a club of three segmented are mostly found in Scarabaeinae. Separated middle coxae, single or mesad two apical spurs present on posterior tibiae, exposed pygidium, and six fused abdominal sternites that are visible are the main keys in Scarabaeinae identification. Sexual dimorphism in Scarabaeinae is often found in certain genera or tribes. For example, in certain *Onthophagus* species male adults have a massive and outstanding horn on their head or pronotum instead of female adults (Kishi et al., 2015). Scarabaeinae is categorised into three

categories based on their feeding and breeding habits: rollers, tunnelers, and dwellers. As roller dung beetles, tribe Sisyphini and Cathonini have elongated, curled middle and posterior tibiae (University of Nebraska-Lincoln, n.d.).

2.2 Ecological Roles of Scarabaeidae

Scarabaeidae's impression in the human community can be inconstant due to Scarabaeidae being notorious as agricultural pests for oil palm plantations, sugar cane plantations, and fruit orchards, while also well known as pollinators, decomposers, and biological indicators. These phenomena are mostly caused by their natural foraging, breeding, and feeding behaviours.

2.2.1 Scarabaeidae as Agricultural Pests

According to Hill (2008) and Wylie and Speight (2012), sugarcane and young plantations in tropical Asia and Australia were reported on massive damaged by grubs of Scarabaeidae. Aside from the grubs, the adult Scarabaeidae like *Popilia japonica*, the Japanese beetle, *Maladera castenea*, the Asiaticgarden beetle, *Amphirhallon majlis*, the European chafer, the genera *Lepidiota*, *Leucopholis*, and *Holotrichia* are representing the most destructive beetles towards living plants due to their phytophagous behaviour (Bandara, 1990; Jameson, 2001). Scarab beetle grubs are agricultural pests because they feed on roots while decaying wood or plant debris is one of their preferred diets. For example, masked chafer (*Cyclocephala* spp.) and Japanese beetle (*Popillia* spp.) were recorded as serious pests attacking corn roots in maize plantations located in Ethiopia (Theshita & Gashaw, 2014), while *Oryctes rhinoceros*, the rhinoceros beetles were notorious oil palm pests in Malaysia for attacking the roots and the newly merge leaves of the palm trees (Gnanasegaram, 2024).

2.2.2 Scarabaeidae as Pollinators

Even though most Scarabaeidae are considered agricultural pests, they are also known as important or primitive pollinators as they differentiated and evolved before the angiosperms (Faegri & Van Der Pijl, 1978; Kevan & Baker, 1983; Paz et al., 2021). Certain Scarabaeidae like Hopliini, monkey beetles with hairy bodies play a crucial function as pollinators for odourless flowers. According to earlier research, the qualities of an appealing flower to monkey beetles are white-coloured petals or black centres that simulate a resting insect, such as *Ixia dubia* and *Spiloxene capensis*. These flowers provide excellent foraging and mating opportunities for pollen-feeding monkey beetles (Picker & Midgley, 1996; Johnson & Midgley, 2001; Goldblatt & Manning, 2011; Hasegawa et al., 2015). According to a study by Shuttleworth and Johnson (2010), several asclepiad, orchid and protea species were frequently visited by some flower chafers (Cetoniinae), such as *Atrichelaphinis tigrina*, *Cyrtothyrea marginalis* and *Leucoscelis* spp. This study suggested that the scent of flowers is an important component for pollination by Cetoniinae. Certain Dynastinae and Cyclocephalini were also documented as scent-oriented pollinators by Maia et al. (2013) in Neotropics which they used the flower of *Taccarum ulei* (Araceae) as a mating aggregation site and fed on the pollens while pollination services as a payback. Not only in Neotropics, but in Thailand, *Peltonotus nasutus*, a Rutelinae member was recorded as a pollinator for *Amorphophallus paeoniifolius* (Araceae). This Rutelinae are highly attracted to and forage on flowers with robust bowl-shaped petals along with fermenting fruit odours (Kaven & Baker, 1983; Sites, 2017). While in Sarawak, Malaysia, Sakai and Inoue (1999) had discovered a new pollination system in *Orchindanta inouei* (Lowiaceae, Zingiberales) with the aid of certain scarabaeid dung beetles mostly from *Onthophagus* and *Paragymnopleurus* genera. In another research of pollination biology in a lowland dipterocarp forest in Sarawak,

Paratasia sp. (Rutelinae) was identified as one of the pollinators that fed on the staminodes and pollen of *Homalomena propinqua* (Araceae) (Momose et al., 1998).

2.2.3 Scarabaeidae as Decomposers

To keep specific ecosystems from becoming overrun with ammonia because of nitrogen and mineral loss from ungraded vertebrate excrement. Scarabaeinae, the dung beetles play an important role in assisting the nutrient cycle during both daytime and night time according to their species (Yokoyama et al., 1991; Hernandez, 2001). Ramli et al. (2019) suggested that dung beetles share the same feeding behaviour as earthworms, excreting waste after consuming organic matter from the humus as dung beetles are detritivores for both larvae and adults. Scarabaeinae can also feed on a variety of invertebrates, including newly killed millipedes and rotting fruits and leaves, in addition to humus and carrion (Forgie et al., 2002). Aside from maintaining the nitrogen cycle, Scarabaeinae that decomposes the vertebrate dungs also inhibits the development of dung-associated invertebrates like dipterans and other parasites that are harmful to humans and vertebrates such as gastrointestinal parasites that breed in vertebrates dungs and infect other mammals (Heo et al., 2010; Floate, 2011). Three functional groups, namely, dwellers, tunnellers, and rollers are classified for the dung beetles according to their breeding behaviour associated with the vertebrate dungs (Cambefort & Hanski, 1991). Most of the dweller dung beetles are from the Aphodiinae subfamily. Dweller dung beetles complete their life phases before adulthood within the dung or between the dung and the soil surface, rather than in chambers or burrows. Adult tunneller and roller dung beetles will take a piece of the excrement and pack it into a tunnel about 10 centimetres underground. Tunneller and roller dung beetles both packs only one egg into each dung chamber when roller dung beetles roll a dung ball while tunneller dung beetles do not (Figure 2.10) (Doube, 1990). In addition,

roller dung beetles also contribute to seed dispersal as they roll the dung balls which might contain undigested seeds (Nichols et al., 2007).

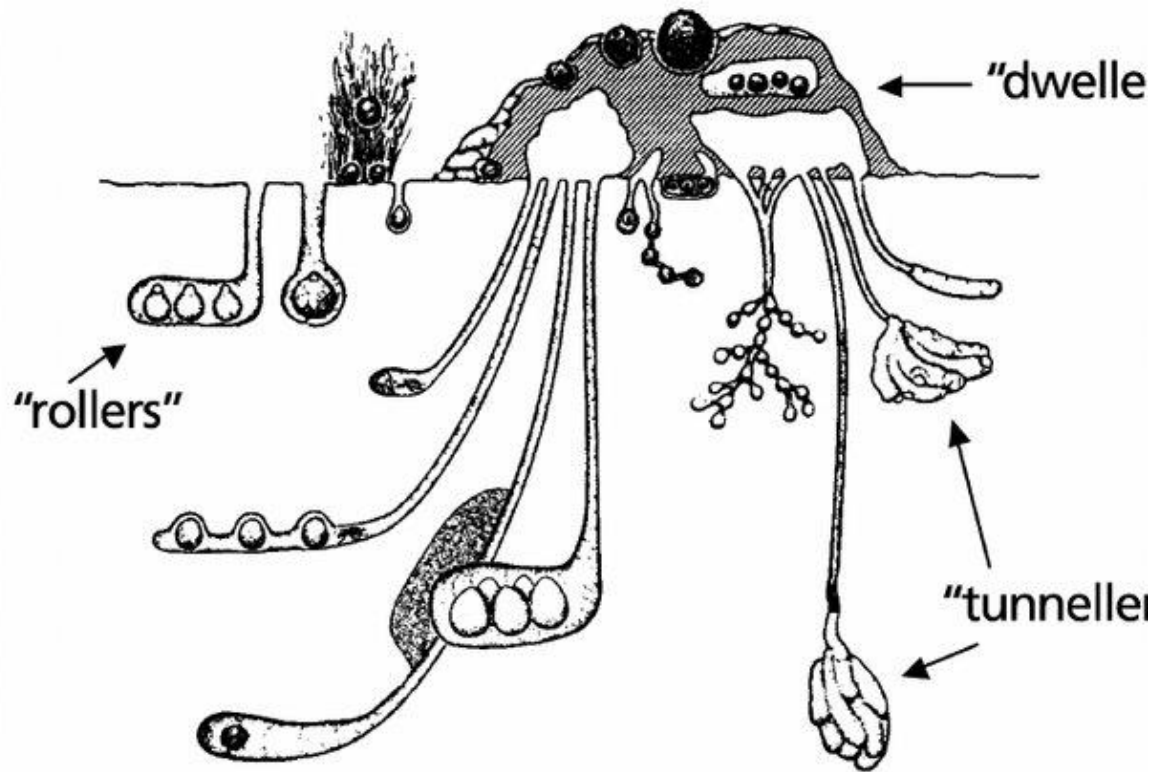


Figure 2.12: The three major classifications of dung beetles according to their breeding behaviour (adapted from Doube, 1990)

2.2.4 Scarabaeidae as Biological Indicators

Bioindicators are used to describe quality changes in specific settings across time through the study or recording of biological processes, species, or communities. Pollution from anthropogenic activities and natural stresses are among the causes contributing to changes in environmental quality (Holt & Miller, 2011). According to Andresen (2003), Scarabaeidae can contribute to the indication of the conservation status of several environments due to their sensitivity to changes in their ecology. Furthermore, because of their high density and speciose family tree, Scarabaeidae has been demonstrated as a viable

subject for bioindication study or research on disruptions in tropical settings or human habitats (Nichols et al., 2007; Slade et al., 2007; Shahabuddin et al., 2010). In a previous study conducted by Shahabuddin et al. in 2014, they suggested that *Copris saundersi* and *Onthophagus forsteni* indicate a less exposed and cooler environment like natural forest and cacao agroforestry, while *Onthophagus limbatus* and *O. trituber* indicate a more exposed and warmer environment. Another study was about the relationship between Scarabaeidae and abiotic factors in an oil palm plantation like carbon dioxide content and soil organic matter (Ramli et al., 2019). Furthermore, Doll et al. (2014) provided a record of Scarabaeidae occurrence and distribution data varied on geographical and environmental data, such as forest size, flora and fauna diversity, elevation, and others.

2.3 Importance of Species Diversity

Species diversity is defined as the taxonomy variety found in certain habitats, continents, or even biomes to the whole biosphere (Kempton, 2002). Species diversity in one habitat can be affected by both biotic and abiotic factors, such as relationships between communities from different species, exposure to sunlight, ventilation, soil organic matter, and others. The study of species diversity is crucial in establishing conservation programs or proposals on specific places or species because it is easier to assess and understand for the public (Kiester, 2013). Instead of comparison status, species diversity also helps researchers to define the difference between flora and fauna diversity between or among localities. In Sabah, beetle assemblages in different forest types like primary forest, logged forest, acacia plantation, and oil palm plantation showed distinctive results in species diversity. Oil palm plantations had the most affected beetle diversity with the dominance of certain species compared to other environments due to different environmental variables (Chung et al., 2000; Lassau et al., 2005).

2.4 Spatial Distribution Modelling

According to Rahman et al. (2018), bias should be avoided between biodiversity conservation and economic development which emphasises the importance of spatial distribution modelling in conservation planning. Spatial distribution modelling, also known as SDM, is a study between occurrence data of certain populations and abiotic environmental conditions in any taxa from terrestrial, freshwater, to marine ecosystems (Scarnati et al., 2009). These provide a foundation for ecologists to predict the spatial distributions in making conservation planning and reserve design (Elith & Franklin, 2017). Additionally, SDM contributes to the production and prediction of current or future potential habitat areas for specific species. For example, Lah et al. (2021) successfully predicted *Melalucea cajuputi* habitat viability for current and future climatic scenarios showed that Setiu and Marang regions had different suitability for *M. cajuputi* for long terms due to climatic conditions. Another study by Zulkeflee et al. (2022) proved that spatial distribution model can be applied in forecasting or predicting spatial distribution of *Piper porphyrophyllum* in Kelantan, Malaysia which suggested that Pulau Chondong and Lala Cuit are ideal habitats for respective species.

2.5 Previous Studies on Beetles' Diversity

In a previous study by Kato et al. (2000), a total of 7,243 scarab beetle individuals and 621 Meloidae beetles were collected using light trapping method in Lambir Hills National Park, Sarawak, Malaysia. This study was conducted to investigate the temporal patterns of light-attracted scarab and meloid beetle diversity according to climate conditions throughout the years. Another study in six different forest types of primary forest, isolated primary forest, rubber gardens, old fallows, young fallows, and new fallows around Lambir Hills National Park by Kishimoto-Yamada et al. (2011) recorded 3,230 individuals from

approximately 51 morpho-species. Throughout the study, isolated primary forests had the highest total species richness while new fallows had the highest abundance although estimated species richness showed less difference among the forest types.

In Peninsular Malaysia, Mustafa and Abdullah (2019) investigated the beetle diversity at Fraser's Hill. A total of 1,981 individuals and 116 different species of beetles from 36 different families were collected. At a 500 m elevation gradient, the most abundant families were Staphylinidae, Scolytidae, and Chrysomelidae, with *Orphnebius* sp. from Staphylinidae being the dominant species. The prevalent species at 1,000 m, 1,500 m, and 1,800 m were *Anomala* sp. from the Scarabaeidae, *Xyleborus* sp. from the Bostrichidae, and *Brachypeplus* sp. from the Nitidulidae, respectively. This study also demonstrated the importance of various microhabitats in completing beetle species assemblages.

Goh et al. (2014) conducted another investigation on the association of beetle with elephant dung in Malaysia's Temenggor Forest. *Corpis numa*, *C. bellator*, *C. doriae*, *Corpis* sp., *Heliocorpis tyrannus*, *Liatongus femoeatus*, and other dung beetle species were gathered. According to the findings of this investigation, there large dung beetles are outnumbering the small dung beetles. Scarabaeidae larvae were also discovered inside the elephant dung. This study added to the body of knowledge about the relationship between dung beetles and large mammals.

A total of 30 individuals from 13 species of Scarabaeidae were collected in the lowland rainforest of Sorong Nature Tourism Park, West Papua, Indonesia. Three sites were surveyed for scarab beetle diversity, which are the rehabilitation zone, conservation zone, and protection zone. In this study, *Onthophagus* spp was recorded with the highest species richness compared to *Aphodius* spp., *Anomala* spp., and *Adoretus* spp.. The protection zone also found as the site with the highest diversity index ($H'=2.09$), while $H'=2$ and $H'=0.5$

were recorded for the conservation zone and rehabilitation zone respectively (Fitradiansyah et al., 2023).

Meanwhile, in Nepal, five farming sites were examined for Scarabaeidae abundance and diversity using light traps for 12 months, a total of 4,708 individuals were collected and 77 species were recorded. *Adoretus coronatus*, *Maladera thomsoni*, *Anomala dimidiata*, *Anomala bilobate*, and *Holotrichia nigricollis* were the top five most common species found in this study along with 58.81% of total capture (Dhoj et al., 2009).

2.6 Threats towards Scarabaeidae

Nowadays, Scarabaeidae diversity facing some threats as the high pace of human development. For example, urbanisation and anthropogenic activities occurring around the globe like the loss of breeding places for female scarab beetles to lay eggs or less fertile substrate for grubs to ingest nutrients. Anthropogenic activities are one of the variables affecting Scarabaeidae dispersion as the dispersion of agricultural pests is facilitated by the plantation of commercial crops (Schowalter, 2011). According to New (2010), two major categories of pollution, human activities' by-products like industrial pollution and pesticides are among the deadly threats to the beetles population. Soil and water pollution might vary conversely to industrial and agricultural development since the surrounding environment at the river might be affected by the consequences of the disposal of industrial waste or heated water into the river might inhibit Scarabaeidae from growing especially grubs that highly rely on soil quality. In the aspect of agriculture, overuse of pesticides is also harmful to the Scarabaeidae populations either non-target effects in the areas or drifted to other places. Besides pesticides applied on crops, the pesticides used on domestic stocks for veterinary purposes are also a significant concern because the pesticide discharge from the livestock through excretion can reach a maximum of 90% of the given avermectins dose either through

feces or urine affecting directly dung feeding beetles like *Onthophagus* spp. or grubs underground. Their effects include an increase in the development period, fatality of grubs, and infertility of the adults of Scarabaeidae (Floate, 1998).

Ivermectin and abamectin are the two major formulations of avermectins used widely (Strong, 1992). Kruger and Scholtz suggested (1997) that the prevention of treatment for cattle in South Africa during the breeding period of South African dung beetles should be considered to avoid the potential risks of ivermectin after emergence comparison of *Euoniticellus intermedius* from dungs between treated and untreated cattle showed a distinct difference. In Australia, the residues of ivermectin in dungs decrease the attraction of *Onthophagus australis* towards them. Especially for some Mediterranean dung beetles which are burrowers like *Corpiss*, *Onitis*, and *Geotrupes*, their exposure to avermectin is longer and more consistent because slower decomposition of dung occurs underground than above the ground. This shows that the decomposition of dung in certain places can be used as an index of avermectin influence after several studies have been conducted (Ridsdill-Smith, 1988; Lumaret et al., 1993; Dadour et al., 1999).

CHAPTER 3

GENERAL METHODOLOGY

3.1 Materials and Methods

3.1.1 Study Site

This study was conducted mainly in the western region of Sarawak, Malaysia including some sites in the northern and center of Sarawak, distanced from Samunsam Wildlife Sanctuary, Lundu Division to Lambir Hill National Park, Miri Division (Table 3.1) (Figure 3.1). These localities include several types of forests like mixed dipterocarp forests, peat swamp forests, limestone forests, mangrove forests as well as heath and littoral forests.

Table 3.1: Localities with forest type and coordinates

Localities	Forest type	Latitude	Longitude
Gunung Gading National Park	Lowland mixed dipterocarp forest	1.6906°N	109.8458°E
Gunung Ngelik	Mixed dipterocarp forest	1.3784°N	110.7895°E
Sebangkoi	Mosaic mixed dipterocarp forest	1.9564°N	111.4326°E
Lambir Hills National Park	Mixed dipterocarp forest	4.1984°N	114.0429°E
Samunsam Wildlife Sanctuary	Mixed dipterocarp forest	1.7215°N	109.7861°E
Gumpey	Mixed dipterocarp forest	1.1021°N	110.3349°E
Niah National Park	Mixed dipterocarp forest	3.8006°N	113.7843°E
Real Living Lab, UNIMAS	Peat swamp forest	1.4656°N	110.4487°E
Loagan Bunut National Park	Peat swamp forest	3.4445°N	114.2272°E
Kampung Serpan Laut	Mangrove forest	1.5615°N	110.6031°E
Adis Buan Resort	Tropical heath forest	1.3231°N	110.0902°E
Sabal Agroforestry	Heath forest	1.0682°N	110.9099°E
Sematan	Littoral forest	1.8083°N	109.7763°E
Mount Serumbu	Limestone forest	1.4254°N	110.2232°E
Gua Temurang	Limestone forest	1.2087°N	110.2709°E
Fairy Cave Nature Reserve	Limestone forest	1.2239°N	110.0711°E
Gua Raya	Limestone forest	1.2363°N	110.4304°E

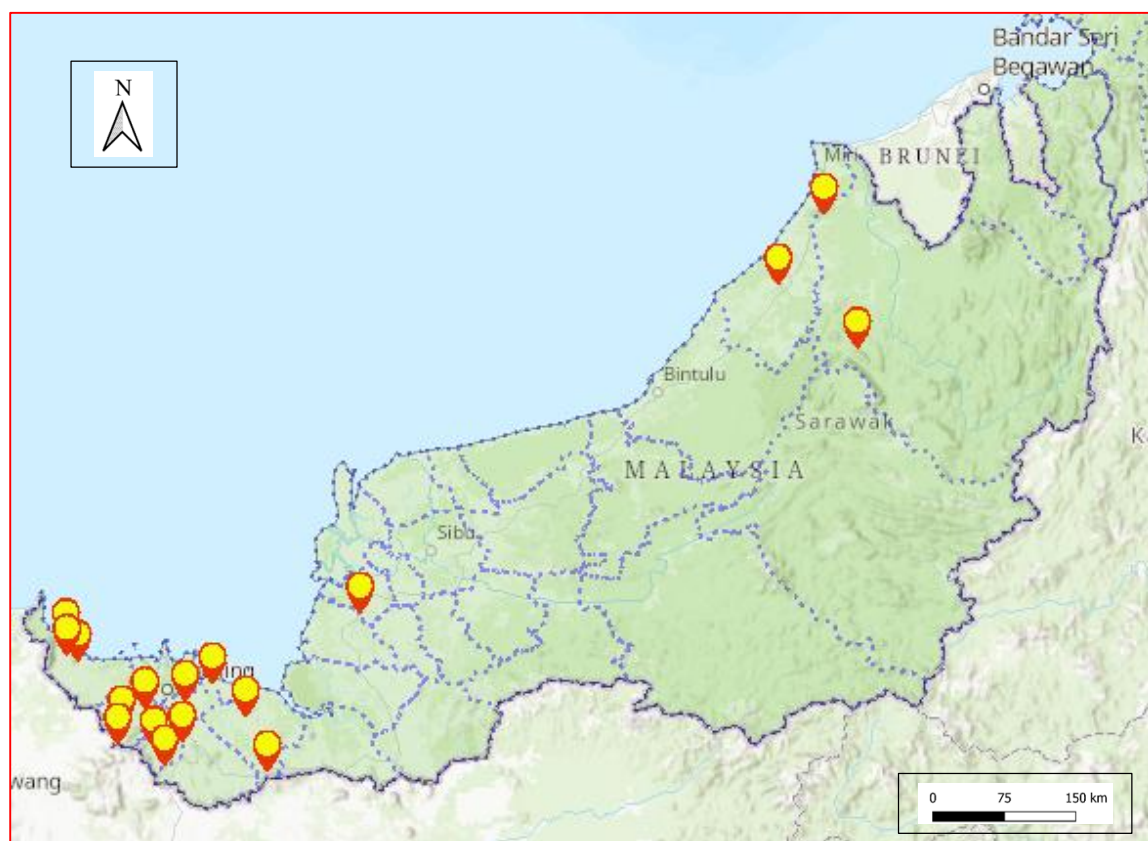


Figure 3.1: Study sites of scarab beetle throughout Sarawak indicated by the yellow-red marking on the map.

3.1.2 Sample Collection

3.1.2.1 Field Sampling

Both active and passive methods were used such as handpicking, aerial nettings (Figure 3.2), Modified Pennsylvanian light traps (MPLT) (Figure 3.3), flight intercept traps (Figure 3.4), and baited traps (Figure 3.5). For active sampling, two collections (0700 to 0900 and 1830 to 2030) by hand picking and aerial netting were done for each sampling day in every site. All scarab beetles encountered on the trails were captured either by hand picking or aerial nettings. After the samples were captured, then were kept in collecting vials. Then the collected scarab beetles were processed and documented properly after being immobilised with a killing jar.

Two modified Pennsylvanian light traps (MPLTs) were deployed at each site with at least 100 m distance between them to avoid interference. Each MPLT was placed at the forest edge with an ethyl acetate-filled killing jar setting from 1800 until 0600 hrs the next morning for five continuous nights. All Scarabaeidae within the MPLTs were sorted and identified until the species level (if possible). Ten flight intercept traps and 10 baited traps were placed in five groups, each about 50 m apart. Baits for flight intercept traps used a mixture of beer with molasses and a mixture of yeast with honey to increase the capture rate of Scarabaeidae with the sweet, strong fermentation fragrant. Meanwhile, those baited traps were filled with pineapples and papaya. During the sampling periods, these traps were only checked every two to three days. Fruit baits were chosen as the baits to trap the scarab beetles due to the previous study by Puker et al. (2020) who found that fruit baits had a high efficiency in attracting Scarabaeidae, particularly Cetoniinae because most of them are phytophagous and have low susceptibility to fragrance from sugarcane with fruit mixes after fermentation.



Figure 3.2: Aerial net

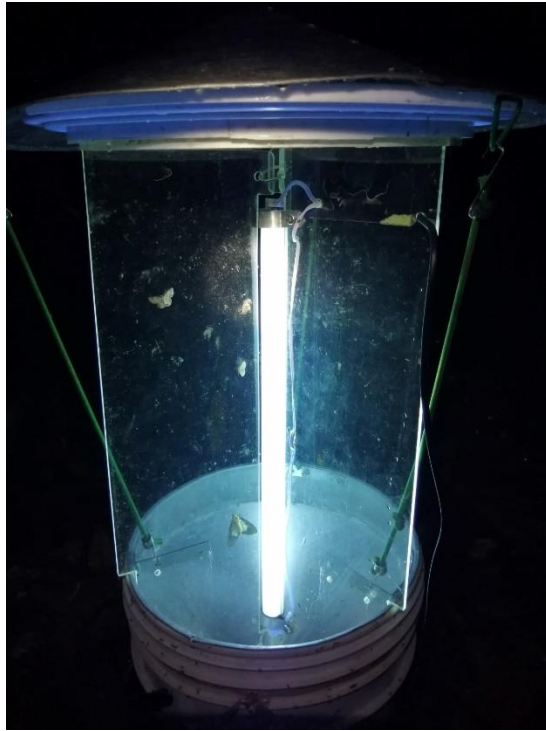


Figure 3.3: Modified Pennsylvanian light trap (MPLT)



Figure 3.4: Flight-intercept trap



Figure 3.5: Baited trap

3.1.2.2 Samples Processing and Identification

There are three steps to process Coleoptera: pinning, labelling, and storing. The beetle specimens were inserted using an insect pin in the right front wing towards the base, and the pin was adjusted to ensure that it was perpendicular and straight. When the pin was properly aligned, it was pushed through the specimen until approximately one-quarter of the pin's length remained above the insect. The insect block was used to keep the specimen and label heights consistent.

For printed labels, a font size of 3 or 4 was used. Labels were parallel to the body of the specimen. The first label on the pin should include the following information: country, state or province, county or parish, nearest town, date of collection, and collector's name. Dates were written as Day-Month-Year (e.g., 20-JUN-1943). The habitat, species name, and method of collection were included on the second label. Then, a pinning block was used to

position labels of equal height on all specimens. Finally, keep the insect collection in wooden storage boxes (insect boxes) or cabinets with trays. The collection was sealed tightly with a fumigant such as naphthalene (mothballs) or paradichlorobenzene to keep pests from destroying it.

To identify the collected Scarabaeidae, several types of sources were reached or accessed. Firstly, physical books like “The Insects of Borneo (including South-east Asia)” and “A Guide to Beetles of Borneo” (Hill & Abang, 2010; Bosuang et al., 2017). Physical books provided an overview of guidance in species identification of Scarabaeidae, together with other descriptions presented with figures. Second, the UNIMAS Insect Reference Collection (UIRC) from the Faculty of Resource Science and Technology, Universiti Malaysia Sarawak was accessed during species identification to provide a better view of Scarabaeidae body structures than from physical books. Lastly, some websites like beetle identification, iNaturalist, and MyBis were accessed to overcome the short information from the previous two sources.

3.1.2.3 Voucher Specimens

Besides sample collection from the field, voucher specimens from UNIMAS Insect Reference Collection, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, and Research Development, and Innovation Division, Forest Department Sarawak, and others for species diversity and spatial distribution study for Scarabaeidae. Details like localities, and date of collection were recorded for further proceedings.

3.1.2.4 Secondary Data

Secondary data from previous studies about Scarabaeidae assemblages conducted in Sarawak were also recorded. For example, a record from Kato et al. (2000), had recorded 80

individuals of *Anomala* species in Lambir Hills National Park. Another collection of around 3,000 individuals from 11 *Apogonia* species in Lambir Hills National Park (Kishimoto-Yamada et al., 2011). Another study by Ismail (2013) in Mount Serumbu showed a difference in biodiversity indices between the lower and upper elevations of Mount Serumbu which made a piece of evidence for the affection of abiotic factors towards beetle diversity.

3.2 Data Analysis

3.2.1 Analysis of Species Diversity

To analyse the species diversity of Scarabaeidae in Sarawak, Microsoft Excel and PAST software version 4.3 were used to calculate the diversity indices like Simpson 1-D and Shannon. Species richness and species evenness were also calculated for each locality with different forest types. A compiled species checklist was prepared to represent the preliminary checklist for Scarabaeidae in Sarawak, Malaysia along with the diversity indices.

3.2.2 Analysis of Spatial Distribution

Before proceeding to the construction of spatial distribution modellings, one genus instead of one species was selected from each subfamily in Scarabaeidae as the species under the same genus mostly share the same behaviour so it might provide better accessibility in gathering occurrence data, for example, *Ixorida* was selected from Cetoniinae, *Chalcosoma* was selected from Dynastinae, *Apogonia* was selected from Melolonthinae, *Anomala* was selected from Rutelinae, and *Onthophagus* was selected from Scarabaeinae. All species under these genera were recorded for their occurrence data in Microsoft Excel, and then the data from Microsoft Excel were uploaded to Maxent together with study site layers constructed by using QGIS and map layers from the WorldClim website

(<https://www.worldclim.org/>) to construct a spatial distribution modelling map or a heat map that predicts the distribution movement over time and space with other components like anthropogenic activities and urbanisation. Several environmental factors data were added to the QGIS in the construction of prediction maps with the affection of respective environmental factors.

CHAPTER 4

DIVERSITY OF SCARABAEIDAE IN SARAWAK

4.1 Introduction

The Scarabaeidae family, also known as scarab beetles, serve important roles in many ecosystems. Sarawak, on the island of Borneo, is home to many scarab beetle species, contributing to a high biodiversity of animal species. Scarabaeidae is known to be beneficial and harmful to natural and human environments. Scarabaeidae has performed many significant ecological and economic functions worldwide, including pollinators, decomposers, biological and environmental indicators, biological control agents, and agricultural pests (Chung, 2007). According to Shahabuddin et al. (2014), changes in environment or habitat conditions can be recognised by Scarabaeidae as bioindicators, allowing for the assessment of the effects of anthropogenic activities on the biota without investigating the entire ecosystem. Furthermore, Harper and Hawksworth (1995) indicated that information on beetle assemblages can provide qualitative and quantitative indices of biodiversity that can be used to make conservation decisions. On the other hand, some beetles are harmful to both the ecosystem and human society for being agricultural pests which significantly cause massive damage to plantations and reduced crop yields.

Diversity study is one of the components to define the environmental health in certain habitats including variations and interactions between living things and ecosystems with the association of biodiversity indices. One habitat's diversity can be affected by biotic and abiotic factors that manipulate birth rate, mortality, distribution, and others (Ment et al., 2017). Lassau et al. (2005) suggested that their food preference highly influences the diversity of beetles in one habitat. For instance, *Oryctes rhinoceros*, from Dynastinae is

notorious as an agricultural pest, especially in oil palm plantations or plants from the Arecaceae family (Manjeri et al., 2014).

The peat swamp forest on the other hand is possibly the most exploited, being the first forest type to be logged in Sarawak for highly valuable timber species (Ipor, 2006). It is one of the most important vegetation types in Sarawak that occurs along the coast on low-lying and poorly drained sites, representing about 13% of the total Sarawak's land (Tawan, 2006). Abang and Hill (2006) also suggested that the peat swamp forest should be recognised as a reservoir for the maintenance of biodiversity, along as one of the important sources of renewable bioresources.

Besides that, the mangrove forest which refers to coastal areas of tropical and subtropical regions plays vital roles in carbon storage, fisheries and biodiversity conservation, including in erosion and flood control as well as in nutrient cycling (Jusoh et al., 2020). However, the total area of mangrove forest in Sarawak is represented by only 1.1% of the State's total land where most are situated in Kuching and Mukah Divisions (Abg Ahmad et al., 2008).

Limestone forest, according to Chargualaf and Salas (2022), is made up of limestone and has flora and fauna as well as shallow and neutral to mildly alkaline soil. According to World Wildlife Fund Malaysia (2018), there were an estimated 26,000 hectares of forested limestone areas, most of which were centred in northern Peninsular Malaysia, while limestone forests covering approximately 50,000 hectares in Sabah and Sarawak.

The heath forest known as “kerangas forest” in Borneo, originated from the Iban language to define the discouragement of paddy plantation and is mostly located between peat swamp and dipterocarp forests. Moreover, heath forests were found to have thin layers

of organic structures on top of the soil layer inhibiting the growth of vegetation diversity as incapable of conserving and gathering nutrients (Maimunah et al., 2018).

This study is conducted due to the insufficient Scarabaeidae species checklists according to different types of forests throughout Sarawak. Besides, there is also a lack of diversity study of Scarabaeidae in Sarawak currently. So, this study's objective is to provide an overview of the diversity of Scarabaeidae in Sarawak, emphasising their ecological value, unique adaptations, and the importance of their existence in the local ecosystem.

4.2 Study Sites

Seventeen localities of sample collections were visited, from Lambir Hills National Park, Miri to Samunsam Wildlife Sanctuary, Lundu which covers several forest types in Sarawak. These include the mixed dipterocarp forest in Lambir Hills National Park, peat swamp forest in Real Living Lab of Universiti Malaysia Sarawak (UNIMAS), mangrove forest in Asajaya, limestone forests in Bau and Padawan as well as heath forest in Sabal Agroforestry (Table 4.1).

In Sarawak, the mixed dipterocarp forests dominate the uphill lands throughout the state, but over-exploitation and forest degradation occur all the time causing a decline in biodiversity and ecological benefits provided by these forests. *Dryobalanops lanceolata* and *Shorea parvifolia* are the major flora found in mixed dipterocarp forests (Lepun & Heng, 2020). Not only economically important to human society, but mixed dipterocarp forests are also ecologically important by providing an environment with a varied diversity of flora and fauna in Sarawak.

Table 4.1: Study sites with code, forest type, and GPS coordinates

Localities	Code	Forest type	Location	
			Latitude	Longitude
Gunung Gading National Park	GGNP	Mixed dipterocarp forest	1.6906°N	109.8458°E
Gunung Ngelik	GN	Mixed dipterocarp forest	1.3784°N	110.7895°E
Sebangkoi	Sbk	Mixed dipterocarp forest	1.9564°N	111.4326°E
Lambir Hills National Park	LHNP	Mixed dipterocarp forest	4.1984°N	114.0429°E
Samunsam Wildlife Sanctuary	SWS	Mixed dipterocarp forest	1.7215°N	109.7861°E
Gumpey	Gp	Mixed dipterocarp forest	1.1021°N	110.3349°E
Niah National Park	NNP	Mixed dipterocarp forest	3.8006°N	113.7843°E
Real Living Lab, UNIMAS	RLL	Peat swamp forest	1.4656°N	110.4487°E
Kampung Serpan Laut	KSL	Mangrove forest	1.5615°N	110.6031°E
Adis Buan Resort	ABR	Tropical heath forest	1.3231°N	110.0902°E
Sabal Agroforestry	SA	Heath forest	1.0682°N	110.9099°E
Sematan	Smt	Littoral forest	1.8083°N	109.7763°E
Loagan Bunut National Park	LBNP	Peat swamp forest	3.4445°N	114.2272°E
Gua Temurung	GT	Limestone forest	1.2087°N	110.2709°E
Fairy Cave Nature Reserve	FC	Limestone forest	1.2239°N	110.0711°E
Gua Raya	GR	Limestone forest	1.2363°N	110.4304°E
Mount Serumbu	MS	Limestone forest	1.4254°N	110.2232°E

4.3 Sample Collection

4.3.1 Field Sampling

At least one field sampling will be conducted on each site for five days respectively. Both active and passive sampling methods were applied to increase the capture rate of the Scarabaeidae population to prevent bias within Scarabaeidae diversity since they preset in both diurnal and nocturnal environments. Two modified Pennsylvanian light traps (MPLTs) were deployed at the forest edges every sampling day from 1800 until 0600 hrs for five consecutive nights. Killing jars with ethyl-acetate were placed in the MPLTs to immobilise the trapped scarab beetles. There was a distance of at least 100 m between the two MPLTs. MPLT mostly purposed to collect phototaxis-positive Scarabaeidae as suggested by Flanders

et al. (2000). Active samplings were conducted to ensure the variety of data collection because not all scarab beetles will be attracted to the traps. Two collections (0700 to 0900 and 1830 to 2030) by hand picking and aerial netting were conducted for each sampling day in every site along the trails.

A total of 10 flight intercept traps were deployed and separated into five groups and located around 50 m away from the main trail with a 50-meter distance between each group and about 1 m above the ground. The mixture of beer with molasses and yeast with honey was used as bait for the flight intercept traps. Same as flight intercept traps, another 10 baited traps were deployed along the trail but with papaya and pineapple baits. Soap water included in the baited traps was used to prevent the scarab beetle from escaping. Various types of baits were used to ensure a higher capture rate of Scarabaeidae because a different scarab beetle might be attracted by different baits.

4.3.2 Voucher Specimens

Vouchers are typical specimens of a species obtained during biological field surveys and research, which are physically put in a collection, curated museum, or institution and accompanied by metadata. It is critical for substantiating biological research findings. Voucher specimens are portions of or completely preserved plants or animals gathered and worked on throughout a study (De Moor, 1996), including the organism's physical characteristics, such as its morphology, anatomy, and sometimes genetic material to provide a physical record that other scientists can examine to verify the identification and characteristics of a particular species. They serve as a basis for taxonomic descriptions, helping establish the identity and classification of organisms. Voucher specimens deposited in the UNIMAS Insect Reference Collection (UIRC), Universiti Malaysia Sarawak and also Research, Development and Innovation Division

(RDID), Forest Department Sarawak's collections were also examined to accumulate data from other localities with different forest types.

4.4 Data Analysis

4.4.1 Diversity Analysis

The collected samples were documented in Microsoft Excel according to localities and forest type, respectively. Then the data sheets will be analysed with the aid of PAST software to obtain the biodiversity indices Biodiversity indices including Simpson 1-D and Shannon H were calculated to define the diversity's values. Species richness (the number of species per sample) and evenness (the measure of the relative abundance of the different species making up richness in an area) are the key components to calculate the biodiversity Simpson 1-D index and Shannon H index. When the Simpson 1-D index is higher, the diversity in the respective locality varies directly.

4.4.2 Similarity Analysis

Jaccard similarity (Equation 4.1) was used to find the shared or distinct member between two data sets from localities and forest types. When the Jaccard similarity is closer to 1, it indicates a higher similarity between the two data sets. For example, the Jaccard similarity between GGNP and RLL is 0.0741 while ABR and RLL have 0.125 in Jaccard similarity, this indicates that there is more shared data between ABR and RLL than GGNP and RLL. Besides similarities between localities, similarities between forest types were also calculated to define the two forest types with the most shared data. The Jaccard similarity is calculated by dividing the sum of shared data from both data sets by the total data in both sets as below,

$$J(A, B) = \frac{|A \cap B|}{|A \cup B|} \quad \text{Equation 4.1}$$

The Jaccard similarity will be 0 if two data sets share nothing while 1 when two data sets are identical (Real & Vargas, 1996; Fletcher & Islam, 2018; Karabiber, 2024).

4.5 Results

4.5.1 Diversity Comparison according to Forest Type

A total of six forest types were classified, of which representing heath forest, limestone forest, littoral forest, mangrove forest, mixed dipterocarp forest, and peat swamp forest, and a total of 1,551 beetle individuals from 126 total species (41 singleton species, 61 confirmed species, and 65 morpho species) were successfully recorded in Sarawak throughout this study (Table 4.2). For the forest type with more sites for survey or sampling, the data from all sites were combined as one data sheet for diversity analysis. Overall, the mixed dipterocarp forest was the most abundant and speciose forest type in this study with an average of around 154 individuals for each site, followed by the littoral forest with 139 total individuals in Sematan while the heath forest with a total of 34 species recorded (Figures 4.1 & 4.2). The heath forest showed the highest indices in the Simpson 1-D and Shannon indices, which were 0.9655 and 3.548, respectively. Additionally, the mixed dipterocarp forest recorded as the second highest indices (Simpson 1-D = 0.926; Shannon = 3.826), followed by limestone forest (Simpson 1-D = 0.922; Shannon = 3.068), littoral forest (Simpson 1-D = 0.9174; Shannon = 3.008), and peat swamp forests with 0.922, 0.9174, and 0.8647 in the Simpson 1-D index and 3.068, 3.008, and 2.514 in the Shannon index respectively. Meanwhile, mangrove forest is classified as the least diverse forest type in Sarawak with 0.7547 and 2.14 in Simpson 1-D and Shannon indices, respectively.

Table 4.2: The diversity indices, Simpson 1-D and Shannon H for each forest types, respectively

Forest type	Code	Total species	Total individuals	Simpson 1-D	Shannon H
Heath forest	HF	34	60	0.9655	3.548
Limestone forest	LsF	33	126	0.922	3.068
Littoral forest	LtF	32	139	0.9174	3.008
Mangrove forest	MF	23	182	0.7547	2.14
Mixed dipterocarp forest	MDF	80	927	0.926	3.286
Peat swamp forest	PSF	23	117	0.8647	2.514
1551					

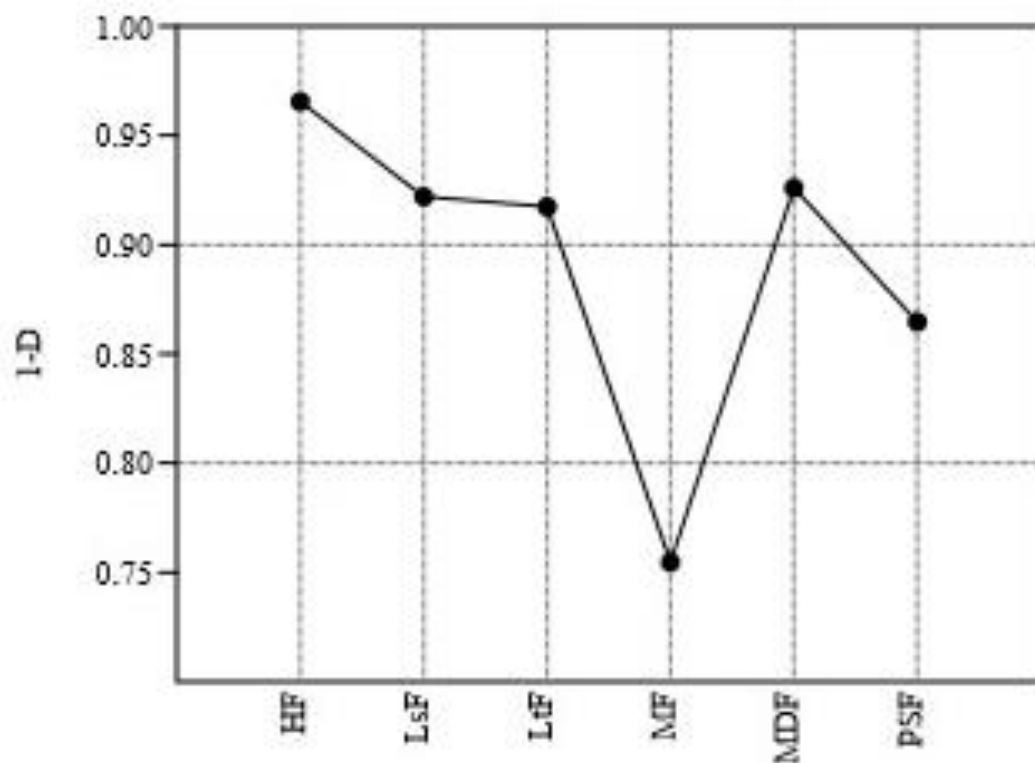


Figure 4.1: Simpson 1-D index against forest type

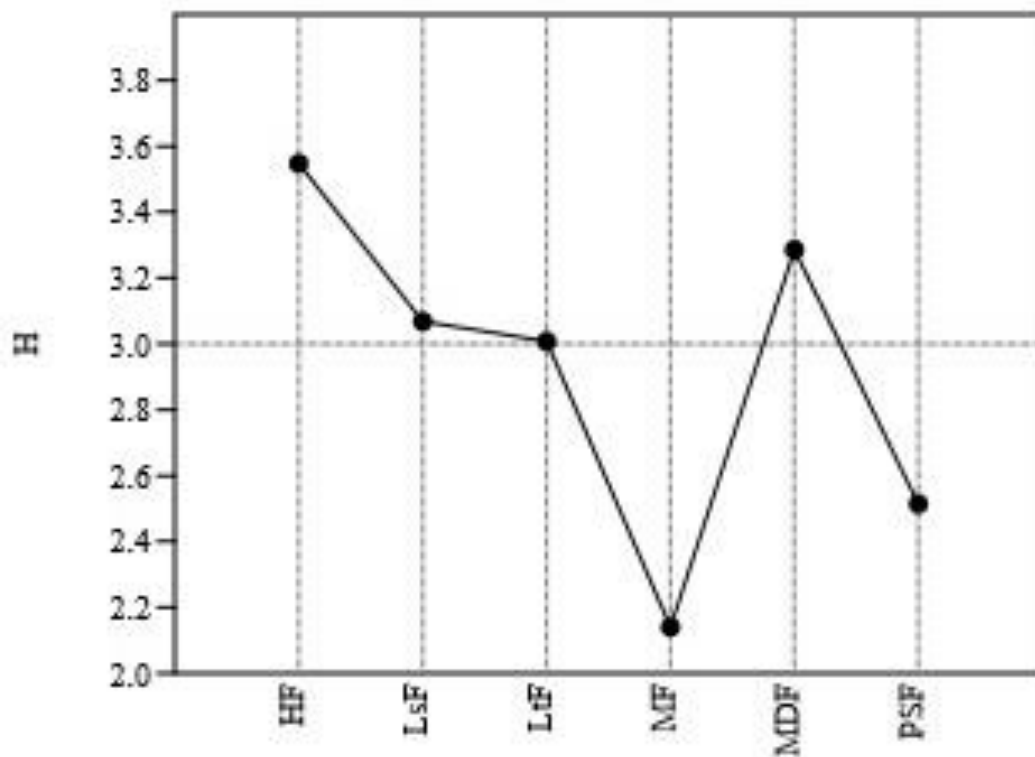


Figure 4.2: Shannon index against forest type

4.5.2 Diversity of Scarabaeidae in Sarawak according to Localities

Among these 17 localities, Samunsam Wildlife Sanctuary has the highest number of samples with 311 individuals collected, followed by Gunung Gading National Park (301 individuals), Sebangkoi (214 individuals), and Sematan (139 individuals), respectively. Besides, in terms of species count, Sebangkoi had the highest amount of species recorded with 46 species, followed by Sematan with 32 species while both Samunsam Wildlife Sanctuary and Sabal Agroforestry had 28 species recorded for each (Table 4.3) (Appendix A).

Table 4.3: The diversity indices, Simpson 1-D and Shannon H for each locality, respectively

Localities	Code	Total species	Total individuals	Simpson 1-D	Shannon H
Gunung Gading National Park	GGNP	21	301	0.7666	2.005
Real Living Lab, UNIMAS	RLL	8	64	0.7128	1.552

Kampung Serpan Laut	KSL	13	80	0.5759	1.480
Adis Buan Resort	ABR	10	14	0.9451	2.527
Mount Serumbu	MS	11	21	0.9333	2.532
Sabal Agroforestry	SA	28	46	0.9546	3.352
Gunung Ngelik	GN	10	50	0.7029	1.671
Sematan	Smt	32	139	0.9174	3.008
Sebangkoi	Sbk	46	214	0.9451	3.326
Loagan Bunut National Park	LBNP	16	53	0.8846	2.461
Lambir Hills National Park	LHNP	12	25	0.8567	2.329
Samunsam Wildlife Sanctuary	SWS	28	311	0.8233	2.348
Gua Temurang	GT	15	58	0.8137	2.161
Fairy Cave Nature Reserve	FC	16	25	0.9323	2.821
Gumpey	Gp	15	102	0.8173	2.138
Gua Raya	GR	14	21	0.9190	2.710
Niah National Park	NNP	16	25	0.9333	2.846
		126	1551		

Overall, Sabal Agroforestry had the highest biodiversity indices (Simpson 1-D = 0.9546; Shannon H = 3.352), followed by Adis Buan Resort (Simpson 1-D = 0.9451; Shannon H = 2.527) and Sebangkoi (Simpson 1-D = 0.9451; Shannon H = 3.326), respectively. On the other hand, the lowest biodiversity indices were reported from Kampung Serpan Laut (Simpson 1-D = 0.5759; Shannon H = 1.480) (Figures 4.3 & 4.4).

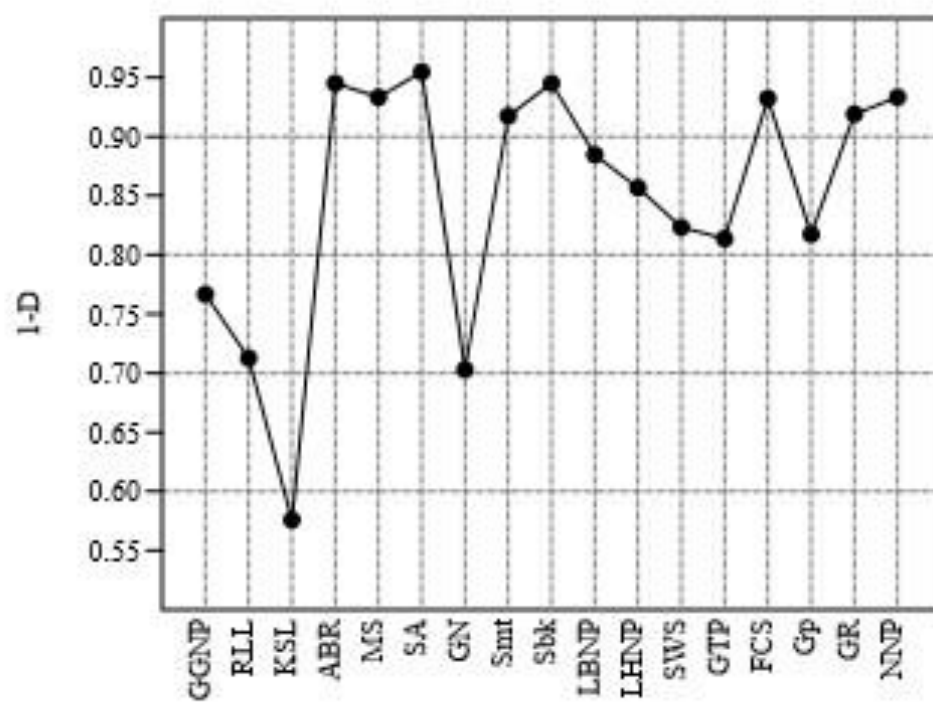


Figure 4.3: Simpson 1-D index against localities

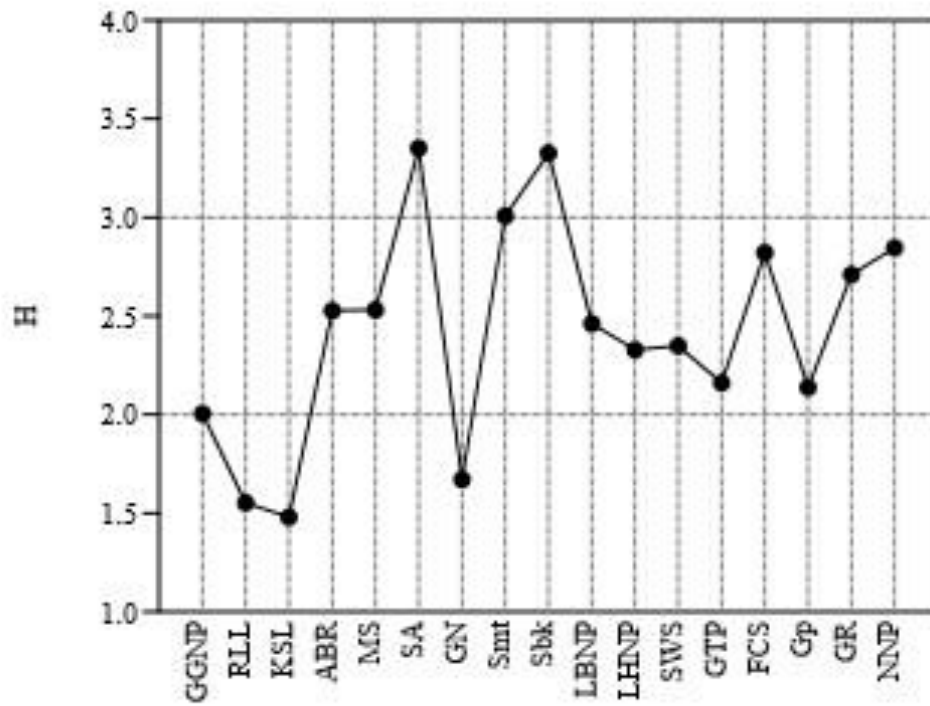


Figure 4.4: Shannon H index against localities

4.5.3 Species Composition of Scarabaeidae in Sarawak

Overall, a total of 126 species of scarab beetles comprising 1,551 individuals from six subfamilies was documented throughout this study (Table 4.4). Melolonthinae represented the most speciose and abundant subfamily of Scarabaeidae recorded, with 49 species (39.99%) and 909 individuals (58.61%), respectively.

Table 4.4: Total species and individuals according to subfamily

Subfamily	Total individuals (%)	Total species (%)
Apodiinae	8 (0.52)	2 (1.59)
Cetoniinae	70 (4.51)	11 (8.73)

Dynastinae	91 (5.87)	10 (7.94)
Melolonthinae	909 (58.61)	49 (39.99)
Rutelinae	242 (15.6)	26 (20.63)
Scarabaeinae	231 (14.89)	28 (22.22)
	1551	126

The second most abundant subfamily was Rutelinae with 242 individuals (15.6%) and 26 species (20.63%), followed by Scarabaeinae with 231 individuals (14.89%) and 28 species recorded (22.22%). From the species level, *Apogonia destructor* from Melolonthinae was recorded as the most abundant species represented by 315 individuals (20.31%). This was followed by *Apogonia* sp.1 and *Onthophagus semiaureus* with 127 (8.19%) and 120 individuals (7.74%), respectively. Throughout the study, *A. destructor* and *Holotrichia serrata* were the most widely distributed species, covering 13 localities out of a total of 17 localities. On the other hand, *A. expeditionis* and *A. waterstradti* were distributed into 11 and 10 localities, respectively. Additionally, the previously mentioned Melolonthinae species, *A. expeditionis* and *A. waterstradti* were found in all recorded forest types.

4.5.4 Jaccard Similarity Test for Forest Types

Limestone forest and mixed dipterocarp forest shared the highest similarity compared to other groups of data sets which was 0.2609 Jaccard index. The result also showed the lowest Jaccard index, 0.1294 happened between mangrove forests and mixed dipterocarp forests (Table 4.6).

Table 4.5: Jaccard similarity test for forest type

	HF	LsF	LtF	MF	MDF	PSF
HF	0	0.1964	0.1579	0.1463	0.17	0.2128
LmF	0.1964	0	0.1404	0.1795	0.2609	0.2444
LtF	0.1579	0.1404	0	0.1842	0.1616	0.1458
MF	0.1463	0.1795	0.1842	0	0.1294	0.2
MDF	0.17	0.2609	0.1616	0.1294	0	0.2045
PSF	0.2128	0.2444	0.1458	0.2	0.2045	0

4.5.5 Jaccard Similarity Test for Localities

In the aspect of localities, GT and GR have 0.381 as the highest reading in Jaccard similarity followed by GR and FC with 0.3636 Jaccard similarity. Which means there were 38.1% of shared diversity occurs between GT and GR while 36.36% of shared diversity between GR and FC. On the other hand, GR and NNP showed the most distinct data sets with 0 Jaccard similarity indicating that there were no shared species found between GR and NNP (Table 4.5).

Table 4.6: Jaccard similarity test for localities

	GGNP	RLL	KSL	ABR	MS	SA	GN	Smt	Sbk	LBNP	LHNP	SWS	GT	FC	Gp	GR	NNP
GGNP	0	0.0741	0.0625	0.1071	0.0667	0.0652	0.069	0.0816	0.1552	0.1563	0.1379	0.2432	0.2	0.2333	0.1613	0.129	0.0571
RLL	0.0741	0	0.1667	0.125	0.1176	0.0909	0.0588	0.0811	0.102	0.0435	0.1111	0.0645	0.0455	0.0909	0.0952	0.1579	0.0909
KSL	0.0625	0.1667	0	0.2105	0.3333	0.1389	0.15	0.1842	0.2041	0.16	0.25	0.2258	0.0769	0.1154	0.2174	0.08	0.0741
ABR	0.1071	0.125	0.2105	0	0.1053	0.1176	0.1111	0.1053	0.098	0.0833	0.1	0.0938	0.087	0.04	0.087	0.0435	0.04
MS	0.0667	0.1176	0.3333	0.1053	0	0.1471	0.1667	0.1316	0.1633	0.125	0.2105	0.2	0.1818	0.1739	0.0833	0.087	0.0385
SA	0.0652	0.0909	0.1389	0.1176	0.1471	0	0.1875	0.1321	0.1746	0.1892	0.1111	0.1277	0.1316	0.1892	0.1316	0.0769	0.1
GN	0.069	0.0588	0.15	0.1111	0.1667	0.1875	0	0.2	0.098	0.1818	0.1579	0.1667	0.1364	0.1818	0.1364	0.0435	0.04
Smt	0.0816	0.0811	0.1842	0.1053	0.1316	0.1321	0.2	0	0.1818	0.1163	0.1579	0.1633	0.119	0.1163	0.1463	0.0977	0.0435
Sbk	0.1552	0.102	0.2041	0.098	0.1633	0.1746	0.098	0.1818	0	0.1923	0.2083	0.2241	0.1731	0.2653	0.1731	0.1538	0.1481
LBNP	0.1563	0.0435	0.16	0.0833	0.125	0.1892	0.1818	0.1163	0.1923	0	0.3333	0.2424	0.1923	0.2308	0.24	0.1538	0.0667
LHNP	0.1379	0.1111	0.25	0.1	0.2105	0.1111	0.1579	0.1579	0.2083	0.3333	0	0.1563	0.1739	0.2727	0.2857	0.1818	0.037
SWS	0.2432	0.0645	0.2258	0.0938	0.2	0.1277	0.1667	0.1633	0.2241	0.2424	0.1563	0	0.2121	0.2059	0.1111	0.1471	0.025
GT	0.2	0.0455	0.0769	0.087	0.1818	0.1316	0.1364	0.119	0.1731	0.1923	0.1739	0.2121	0	0.2917	0.1538	0.381	0.067
FC	0.2333	0.0909	0.1154	0.04	0.1739	0.1892	0.1818	0.1163	0.2653	0.2308	0.2727	0.2059	0.2917	0	0.2917	0.3636	0.1034
Gp	0.1613	0.0952	0.2174	0.087	0.0833	0.1316	0.1364	0.1463	0.1731	0.24	0.2857	0.1111	0.1538	0.2917	0	0.2083	0.1481
GR	0.129	0.1579	0.08	0.0435	0.087	0.0769	0.0435	0.0977	0.1538	0.1538	0.1818	0.1471	0.381	0.3636	0.2083	0	0
NNP	0.0571	0.0909	0.0741	0.04	0.0385	0.1	0.04	0.0435	0.1481	0.0667	0.037	0.025	0.067	0.1034	0.1481	0	0

4.6 Discussion

4.6.1 Diversity of Scarabaeidae according to Localities

The obtained results indicated that species diversity was highly correlated to sampling methods and sample size (Walker et al., 2016). In this study, although Samunsam Wildlife Sanctuary had the highest total of individuals collected, the Sabal Agroforestry had the highest species diversity with lower individual abundance among all localities, which is likely due to the different forest types among all those localities.

As Soetaert and Heip (1990) stated, inaccurate diversity indices are possibly the consequences of varied sample sizes from different localities. Although the sample sizes varied widely throughout all localities, this does not indicate that Sabal Agroforestry had the most diverse scarab beetles community. However, Sabal Agroforestry was highlighted with the highest diversity indices in this study since. This may be due to it is known as a forest reserve and heath forest. The trees in heath forests, despite their relatively small size and the poor nutrient environment and slightly acidic substrates, exhibit a diversity that could contribute to the efficient collection of different types of scarab beetles during field sampling (Othman et al., 2023).

The lowest biodiversity indices were reported from Kampung Serpan Laut. The increasing human population and activities in Kampung Serpan Laut and Adis Buan Resort, such as agricultural development, logging, deforestation and the construction of tourism destinations may influence species abundance and diversity in certain areas. Habitat destruction occurred along with human activities that overexploited the natural environment. The drastic changes in vertebrate composition led to a cascading effect on scarab beetles

communities particularly dung beetle communities which are ecologically important to tropical ecosystems (Slade et al., 2007; Raine & Slade, 2019; Fuzessy et al., 2021).

A variety of vegetation types can be found in Samunsam Wildlife Sanctuary, Sarawak including mangrove, riverine, mixed dipterocarp, and kerangas forest which provide an ideal environment for Scarabaeidae to disperse (Hazebroek & Abang Morshidi, 2000; Mohd-Azlan et al., 2022). The high abundance of Scarabaeidae in this area can also be a consequence of the establishment of Samunsam Wildlife Sanctuary as a conservation site for proboscis monkeys (*Nasalis larvatus*) populations (Mohd-Azlan et al., 2022). As a result, certain Scarabaeidae species like *Onthophagus semiaureus* serve as decomposers due to their feeding behaviour and are highly attracted to their trace of life like faeces or decaying foods in Samunsam Wildlife Sanctuary (Gruber, 2012).

4.6.2 Diversity Comparison according to Forest Type

Sarawak is located on Borneo Island near the equator and is mostly landscaped by tropical rain forests including mixed dipterocarp forest, limestone forest, heath forest, and others. Tropical rainforests are categorised as forests with the most diverse flora and fauna (UC Museum of Paleontology, 2019). However, limestone forests such as Mount Serumbu, Gua Temurang, Fairy Cave, and Gua Raya were found to have less abundant but above average diversity of Scarabaeidae communities compared to certain types of forests, particularly dipterocarp forests. The high endemism in plant diversity in limestone forests due to distinctive environmental factors might be a discouragement for Scarabaeidae communities from dispersing there since out of resources for Scarabaeidae to undergo their routine (Long & Trien, 2019; Tolentino et al., 2020).

According to Othman et al. (2023), there are distinctive differences between tropical heath forests and other forest types in aspects of the physical and chemical properties of the substrate. For instance, the vegetation found in heath forests has smaller or narrower diversity due to lower nitrogen levels which inhibit the vegetation diversity expansion and productivity of the Scarabaeidae community. This results in a low abundance of Scarabaeidae in Adis Buan Resort and Sabal Agroforestry. On the other hand, the presence of large saplings, small poles, and shorter trees in heath forests might increase the capture rate of modified Pennsylvanian light traps by providing better visibility for various phototaxis-positive Scarabaeidae species towards the light sources (Syuharni et al., 2014).

From the result, the mixed dipterocarp forest was recorded to have the most abundant and diverse Scarabaeidae community. The rich and rare diversity of fauna and flora also resulted in an extremely complex ecosystem with more than 5,000 beetle species including Scarabaeidae (Demies et al., 2019). For example, Lambir Hills National Park is a well-known mixed dipterocarp forest in Miri, Sarawak is noted for studies on the animal-plant association between an orchid plant, (*Orchidanta inouei*) and some Scarabaeidae species, (*Onthophagus* sp). These Scarabaeidae were found as pollinators for the respective flowers due to the pollen they carried. Besides *Onthophagus* species, *Paragymnopleureus* species were also collected from within the flower petals but pollen was absent on their body surfaces.

4.6.3 Species Composition of Scarabaeidae in Sarawak

In terms of species abundance and distribution, the subfamily Melolonthinae mostly occupied the study areas. For instance, *Apogonia destructor* was recorded as the most abundant and widely distributed species in this study. Melolonthinae is the largest subfamily within Scarabaeidae, and both larvae and adults of Melolonthinae species are notorious

agricultural pests due to their foraging behaviour (Ali et al., 2016). According to Lawrence and Britton (1994) and Rainio and Niemela (2009), the relatively numerous subfamily Melolonthinae serves as a good biological indicator for measuring species diversity because of its nocturnal behaviour and attraction to light traps.

4.7 Conclusion

In conclusion, the diversity of Scarabaeidae from one locality relies on the sampling methods and sample size collected. Although a small sample size was recorded in Sabal Agroforestry compared to other localities, the species recorded is over 50 percent of the sample size which led to the highest diversity indices calculated in this study. On the other hand, heath forests were concluded as the most diverse forest type in this research. Improved or additional sampling methods and standardised sample sizes are recommended to obtain a more comprehensive finding.

CHAPTER 5

DISTRIBUTION MODELLING OF SELECTED BEETLES (SCARABAEIDAE) IN SARAWAK

5.1 Introduction

Sarawak is known to have various types of forests across the state, ranging from mountains, hills to coastal areas. The spatial distribution of Scarabaeidae in Sarawak might be influenced by a combination of environmental factors, including climate, humidity, precipitation, and others as many scarab beetle species in Sarawak are associated with forest ecosystems. For example, lesser Scarabaeinae can be found in limestone forests due to less fertile substrate compared to mixed dipterocarp forests. Some Scarabaeidae can be found in places or environments with higher latitudes, such as *Chalcosoma* sp. In contrast, some scarab beetles like *Oryctes rhinoceros* and *Cyclocephala* sp are adapted to anthropogenic landscapes, including agricultural areas like oil palm plantations and maize plantations. Certain species like *Onthophagus* sp. may be found in proximity to crops, utilising organic matters like crop residues or dung from domestic animals.

Topography is also an important component in affecting the spatial distribution of Scarabaeidae. Different species may be adapted to specific elevations within the varied topography of Sarawak, ranging from lowland areas to highland regions. Scarabaeidae can exhibit preferences for specific microhabitats within larger ecosystems. For example, certain species may be associated with rotting logs, while others prefer decaying vegetation on the forest floor. Sarawak's tropical climate, with high temperatures and humidity, provides ideal circumstances for the diversity of scarab beetles. Different species may have evolved to specific environmental conditions, influencing their distribution throughout the region.

Human activities, such as deforestation, land-use changes, and urbanisation, can significantly impact the spatial distribution of scarab beetles. Some species may thrive in disturbed habitats, while others may be more sensitive to environmental changes. Interactions with other species, including host plants, other insects, and predators, can influence the spatial distribution of scarab beetles. Some species may have specific associations with certain plants or animals, affecting their presence in particular areas. Some species may have specific associations with certain plants or animals, affecting their presence in particular areas, such as, *Synapsis* sp found to be high rely on large mammals for their excrement.

The Spatial Distribution Model (SDM) is a statistical model built using the occurrence of certain populations or phenomena and environmental data with the aid of GIS technology to predict the distribution of populations or phenomena across space which is one of the most effective tools for conservationists. It is useful as the SDM in MaxEnt software offering an association model of the environmental conditions that complete ecological demands and then anticipate the dispersion of individuals (Ravan, 2003; Schowalter, 2011). The shortage of information on spatial distribution for certain populations has always been an obstacle in managing biodiversity conservation. According to Heliövaara and Väisänen (1993), Coleoptera is one of the insect orders that susceptible to pollution, especially families of Carabidae and Staphylinidae which react to toxicity, while Elmidae as bioindicators for aquatic environments. Eggs of terrestrial insects may also be affected directly by pollutants, not to mention the grubs of Scarabaeidae which are known as one of the most efficient filter feeders other than earthworms. Thus, SDM on Scarabaeidae also has the potential to indicate whether pollution occurs or conservation requirements in certain areas (Eberhardt & Thomas, 1991).

Hence, this study aims to map the spatial distribution of selected scarab beetles, namely, *Ixorida* sp. (Cetoniinae), *Chalcosoma* spp. (Dynastinae), *Apogonia* spp. (Melolonthinae), *Anomala* spp. (Rutelinae), and *Onthophagus* spp. (Scarabaeinae), as well as to identify potential high biodiversity and suitability areas that corresponds to these beetle species.

5.2 Methodology

All present occurrence data were recorded and documented from field samplings as mentioned in Chapters 3 and 4. Voucher specimens (mentioned in Chapter 4) from the UNIMAS Insect Reference Collection (UIRC), Universiti Malaysia Sarawak, and Research Development, and Innovation Division (RDID), Forest Department Sarawak were also considered in this study. Microsoft Excel was used to document and sort the recorded data before proceeding to be analysed using Quantum Geographic Information System (QGIS) and MaxEnt softwares to construct the spatial distribution models for selected genera.

5.2.1 Historical Data

Historical data provide a physical record that can be examined by other scientists to verify the identification and characteristics of a particular species. They serve as a basis for taxonomic descriptions, helping to establish the identity and classification of organisms. Most historical data can be obtained from various types of sources, for example, museums, institutions, and forestry departments. Like voucher specimens, historical data can provide distribution data as they aid in constructing a predictive distribution map. Not only physical data or specimens included in historical data, but secondary data from previous study in journal or articles can be included as historical data for constructing of spatial distribution modelling.

5.2.2 Spatial Distribution Analysis

Microsoft Excel, QGIS software, and MaxEnt were used in this research to compute the predictive distribution maps for all the selected genera together with the environmental variables' layers (Table 5.1) like temperature seasonality, precipitation seasonality, precipitation of the warmest month, and others. downloaded from WorldClim.com. The distribution maps show a probability score ranging from 0 to 1 will indicate the probability of presence from low to high. Other than predictive maps, the charts for the responding curve of selected genera toward environmental variables were also presented to determine which is the most important variables in the process of distribution. The ROC curve with corresponding AUC values indicated the model performance, of which AUC value that is larger than 0.7 is considered potentially significant (Elith et al., 2011).

Table 5.1: A list of environmental variables used in the study

Code	Environmental variables	Unit
Bio1	Annual Mean Temperature	°C
Bio2	Mean Diurnal Range (Mean of monthly (max. temp. – min. temp.))	°C
Bio3	Isothermality ((Bio2/Bio7)x 100)	-
Bio4	Temperature Seasonality (standard deviation x 100)	°C
Bio5	Max. Temperature of Warmest Month	°C
Bio6	Temperature Annual Range (Bio5 – Bio6)	°C
Bio7	Min. Temperature of Coldest Month	°C
Bio8	Mean Temperature of Wettest Quarter	°C
Bio9	Mean Temperature of Driest Quarter	°C
Bio10	Mean Temperature of Warmest Quarter	°C
Bio11	Mean Temperature of Coldest Quarter	°C
Bio12	Annual Precipitation	mm
Bio13	Precipitation of Wettest Month	mm
Bio14	Precipitation of Driest Month	mm
Bio15	Precipitation Seasonality (Coefficient of Variation)	-

Bio16	Precipitation of Wettest Quarter	mm
Bio17	Precipitation of Driest Quarter	mm
Bio18	Precipitation of Warmest Quarter	mm
Bio19	Precipitation of Coldest Quarter	mm
Borneo alt.	Altitude or elevation of Borneo island	m

5.3 Results

A total of 202 occurrence data of Scarabaeidae species (Table 5.2) (Appendix C) were represented by *Ixorida* sp. from Cetoniinae, *Chalcosoma* spp. from Dynastinae, *Apogonia* spp. from Melolonthinae, *Anomala* spp. from Rutelinae, and *Onthophagus* spp. from Scarabaeinae from 1979 until 2023 from voucher specimens and historical data as mentioned in above.

Table 5.2: A list of occurrence data for selected genera in Sarawak

Subfamily	Division	Localities	Latitude	Longitude	Year	Reference
<i>Species</i>						
Cetoniinae						
<i>Ixorida</i> sp.						
	Kuching	Batu Kawa	1.5143	110.3272	2014	UIRC
		Dered Krian National Park	1.3802	110.1632	2023	UIRC
		Gua Temurang	1.2087	110.2709	2022	UIRC
					2016	UIRC
		Tasik Biru	1.4139	110.1511		
	Miri	Bukit Durang	3.45	113.8	2014	UIRC
			3.7775	114.2272	2021	UIRC
		Loagan Bunut National Park				
		Niah National Park	3.8006	113.7843	2022	UIRC
		Saremas 2 Fragemented Forest	3.4332	113.778	2015	UIRC
	Samarahan	Gumpey Gedong	1.1021	110.3349	2021	UIRC
			1.4607	110.4509	2016	UIRC
		Kampus Timur, UNIMAS				
		PITAS, UNIMAS	1.4711	110.4347	2016	UIRC
		Sabal Agroforestry Centre	1.06822	110.9099	2021	UIRC
		UNIMAS	1.4667	110.4251	2007, 2010, 2016	UIRC

	Sarikei	Sebangkoi	1.9564	111.4326	2021	UIRC
Dynastinae						
<i>Chalcosoma</i> sp.						
	Bintulu	Bintulu	3.1739	113.0428	1988	RDID
		Jelalong Sungai Mayap	3.1666	113.7	2000	RDID
	Kapit	Belaga Town	2.705	113.7822	1994	UIRC
		Bukit Semalong	2.9318	114.05	1985	RDID
		House Mt.	2.0167	112.9333	1987	RDID
		Long Urum	2.9756	114.2235	1999	RDID
		Ng. Bebangsan	2.1718	113.4374	2003	RDID
		Sungai Amang	2.0021	112.9805	2003	RDID
		Sungai Keluan	2.4167	114.9333	2002	RDID
		Sungai Mujan	1.7833	112.25	1989	RDID
		Sungai Tegulang	2.7	114.2	1994	UIRC
		Ulu Putai	1.8379	113.6167	2001	RDID
	Kuching	Adis Buan	1.5423	110.1515	2019	UIRC
		Annah Rais	1.1329	110.2675	2016	UIRC
		Fairy Cave	1.2239	110.0711	2022	UIRC
		Gua Temurang	1.2087	110.2709	2022	UIRC
		Gunung Gading National Park	1.6906	109.8458	2002, 2016, 2017,	UIRC

				2020	
	Gunung Serapi, Matang	1.5833	110.1833	1979	RDID
	Kampung Sapit	1.1765	110.1976	2023	UIRC
	Kampung Sira	1.1949	110.4055	1995	UIRC
		1.6128	110.1969	2015,	RDID
	Kubah National Park			2016	
	Kuching Waterfront	1.5593	110.3461	2016	UIRC
	Libiki Bamboo Resort	1.3328	110.1061	2019	UIRC
	Lintang Park, Batu Lintang	1.5349	110.3512	2018	UIRC
	Lundu	1.6714	109.852	2016,	UIRC
				2017	
	Matang	1.5734	110.2771	2016	UIRC
	Mount Serumbu	1.4254	110.2232	2021	UIRC
		1.7215	109.786	1994,	UIRC
	Samunsam Wildlife Sanctuary			2021	
	Semantan	1.8083	109.7763	2021	UIRC
	Sempadi Forest Reserve	1.4655	110.4185	2011	RDID
Limbang	Ekspedisi Paya Maga Lawas	4.4453	115.4971	2010	RDID
	Lawas	4.8613	115.4068	1992	RDID
Miri	Beluru Forest Kom	3.983	114.1	1987	RDID
				2003, 2005, 2011, 2014,	
	Lambir Hills National Park	4.1984	114.0429	2015	RDID

		3.7775	114.2272	2012,	UIRC
	Loagan Bunut National Park			2021	
	Mount Dulit	3.3333	114.15	1990	RDID
	Mulu National Park	4.0921	114.8958	1986	RDID
	Niah FR	3.6667	113.6833	1988	RDID
	Niah Res Station	3.7356	113.7808	1984	RDID
Mukah	SMK Matu	2.6692	111.5405	2019	UIRC
Samarahan	Academia Lane	1.4723	110.4215	2016,	UIRC
				2019	
	Desa Ilmu	1.4529	110.4575	2017	UIRC
	External Lab, UNIMAS	1.4681	110.4473	2018	UIRC
	FSGK, UNIMAS	1.4638	110.428	2017	UIRC
	Gunung Ngelik	1.3784	110.7895	2021	UIRC
	Kampus Timur, UNIMAS	1.4607	110.4509	2017	UIRC
	Kolej Allamanda, UNIMAS	1.4643	110.4311	2019	UIRC
	Kolej Bunga Raya, UNIMAS	1.4597	110.4398	2017	UIRC
	Kolej Cempaka, UNIMAS	1.4653	110.4323	2018	UIRC
	Kolej Rafflesia, UNIMAS	1.4463	110.4551	2016	UIRC
	Kota Samarahan	1.4599	110.4883	2002, 2013	UIRC
	PITAS, UNIMAS	1.4711	110.4347	2017, 2019	UIRC
	Sabal Agroforestry Centre			1997, 1999, 2000, 2010, 2011,	UIRC, Kishimoto-Yamada et al. (2011)
		1.06822	110.9099	2021	

	Stadium UNIMAS	1.4613	110.4371	2017	UIRC
	Sebuyau, Simunjan	1.5167	110.9333	2015	RDID
	Unijaya	1.4594	110.4329	2016	UIRC
				1997, 1998, 1999, 2000, 2002, 2003, 2013, 2016, 2017, 2018,	
	UNIMAS	1.4667	110.4251	2019	UIRC
Sarikei	Jalau Ng Ju	2.0167	111.9167	1988	RDID
Serian	Ranchan	1.1486	110.5817	2016, 2017	UIRC
	Ranchan Recreational Park	1.1432	110.584	2016, 2017, 2019	UIRC
	Serian	1.167	110.5665	2016	UIRC
Sibu	Igan Rassau	2.6032	111.8339	2001	RDID
Sri Aman	Kelingkang	1	111.45	2001	RDID
	Lanjak Entimau WIS	1.517	112.167	1992	RDID
	Sungai Balat, Ulu Engkari	3.7236	114.1823	1989	RDID
	Ulu Batang Ai	1.10466	111.8833	2000	RDID

Melolonthinae

Apogonia sp.

Bintulu	Similajau National Park	3.3483	113.1564	1999	UIRC
	Nanga Bawai	2.0085	113.0894	2024	UIRC
Kuching	Adis Buan Resort	1.3231	110.0902	2021	UIRC
	Dered Krian National Park	1.3802	110.1632	2023	UIRC
	Fairy Cave	1.2239	110.0711	2022	UIRC
	Gua Temurang	1.2087	110.2709	2022	UIRC
	Mount Serumbu	1.4254	110.2232	2021	UIRC
	Samunsam Wildlife Sanctuary	1.7215	109.786	2021	UIRC
	Semantan	1.8083	109.7763	2021	UIRC
Miri	Lambir Hill National Park	4.1984	114.0429	2003, 2005, 2021	UIRC, Kishimoto-Yamada et al. (2011)
	Loagan Bunut National Park	3.7775	114.2272	2021	UIRC
Samarahan	Gua Raya	1.2363	110.4304	2021	UIRC
	Gumpey Gedong	1.1021	110.3349	2021	UIRC
	Gunung Ngelik	1.3784	110.7895	2021	UIRC
	Kampung Serpan Laut	1.5615	110.6031	2020	UIRC
	Real Living Lab, UNIMAS	1.4656	110.4487	2020	UIRC
	Sabal Agroforestry Centre	1.06822	110.9099	2021	UIRC
	Sabal Logging Camp	1.3939	110.7523	2000	UIRC

Sarikei	Sebangkoi	1.9564	111.4326	2021	UIRC
Sri Aman	Ulu Batang Ai	1.10466	111.8833	2000	UIRC

Rutelinae

Anomala sp.

Betong	Kampung Serabang	1.9333	109.65	2016	UIRC
Bintulu	Bintulu	3.1739	113.0428	1988	RDID
	Similajau National Park	3.3483	113.1564	1999, 2000, 2002	RDID
Kapit	Kapit Mujong Seringin	2.1797	113.5158	2003	RDID
Kuching	Adis Buan Resort	1.3231	110.0902	2021	UIRC
	Bako National Park	1.7167	110.4667	1984	RDID
	Dered Krian National Park	1.3802	110.1632	2023	UIRC
	Fairy Cave	1.2239	110.0711	2022	UIRC
	Gua Temurang	1.2087	110.2709	2022	UIRC
	Gunung Gading National Park	1.6906	109.8458	2020	UIRC
	Oil palm plantation Sematan	1.8083	109.7763	2012	RDI
	Samunsam Wildlife Sanctuary	1.7215	109.786	2021	UIRC
	Semantan	1.8083	109.7763	2021	UIRC
	Sematan Mangrove Forest	1.8136	109.7897	1979	RDID
	Stadium Sarawak, Kuching	1.5885	110.3602	2016	UIRC
	Wind Cave, Bau	1.4148	110.1377	2016	UIRC

Miri		4.1984	114.0429		
	Lambir Hills National Park			1992-1998, 2003, 2005	Kato et al. (2000), Kishimoto-Yamada et al. (2011), RDID
		3.7775	114.2272	2021	UIRC
	Loagan Bunut National Park				
	Ng. Mabau	2.8	113	2002	RDID
	Niah National Park	3.8006	113.7843	2022	UIRC
Samarahan		1.4678	110.446	2017	UIRC
	Arboretum, UNIMAS				
	Desa Ilmu	1.4529	110.4575	2016	UIRC
	FRST, UNIMAS	1.4696	110.4282	2016	UIRC
	Gumpey Gedong	1.1021	110.3349	2021	UIRC
		1.4519	110.3979	2017	UIRC
	Kampung Merdang Lumut, Kota Samarahan				
		1.5615	110.6031	2020	UIRC
	Kampung Serpan Laut				
		1.4607	110.4509	2016	UIRC
	Kampus Timur, UNIMAS				
		1.4643	110.4311	2016	UIRC
	Kolej Allamanda, UNIMAS				
	Kolej Dahlia, UNIMAS	1.4726	110.4297	2017	UIRC

	Kolej Rafflesia	1.4463	110.4551	2016	UIRC
	Kota Samarahan	1.4599	110.4883	2016	UIRC
	PITAS, UNIMAS	1.4711	110.4347	2016	UIRC
		1.3939	110.7523		RDID
	Sabal Forest Reserve			1997, 1998, 2000, 2002	
	Unigarden	1.4584	110.4105	2016	UIRC
	UNIMAS	1.4667	110.4251	2016	UIRC
		1.4493	110.4552	2017	UIRC
	Vista Ilmu, Kota Samarahan				
Sarikei	Sebangkoi	1.9564	111.4326	2021	UIRC
	Tanjung Manis	2.1764	111.2033	1995	RDID
Serian	Gua Raya	1.2363	110.4304	2021	UIRC
		1.1432	110.584	2016	UIRC
	Ranchang Recreational Park				
Sibu	Selangau, Sarawak	2.5243	112.3249	1999	RDID
Sri Aman	Lanjak Entimau	1.517	112.167	1993	RDID
	Ulu Batang Ai	1.10466	111.8833	2000	RDID
		3.7236	114.1823	1989	RDID
	Ulu Engkari, Sg Balat				

Scarabaeinae

Onthophagus

sp.

Kuching		1.3802	110.1632	2023	UIRC
	Dered Krian National Park				
	Fairy Cave	1.2239	110.0711	2022	UIRC
	Gua Temurang	1.2087	110.2709	2022	UIRC
		1.6906	109.8458	2020	UIRC
	Gunung Gading National Park				
		1.7215	109.786	2021	UIRC
	Samunsam Wildlife Sanctuary				
	Semantan	1.8083	109.7763	2021	UIRC
Miri		4.0921	114.8958	1983	Hanski (1983)
	Gunung Mulu National Park				
		3.7775	114.2272	2021	UIRC
	Loagan Bunut National Park				
		4.1984	114.0429	1999,	
	Lambir Hill National Park			2021	Sakai & Inoue (1999), UIRC
	Niah National Park	3.8006	113.7843	2022	UIRC
Samarahan		1.4656	110.4487	2020	UIRC
	Real Living Lab, UNIMAS				
		1.06822	110.9099	2021	UIRC
	Sabal Agroforestry Centre				
Sarikei	Sebangkoi	1.9564	111.4326	2021	UIRC
Serian	Gua Raya	1.2363	110.4304	2021	UIRC

Based on figures 5.1 until 5.5, the models predicted that most of the high suitability areas for Scarabaeidae were in the southern part of Sarawak and along the coastal area of Sarawak, especially *Onthophagus* spp. and *Apogonia* spp. from Scarabaeinae and Melolonthinae, respectively.

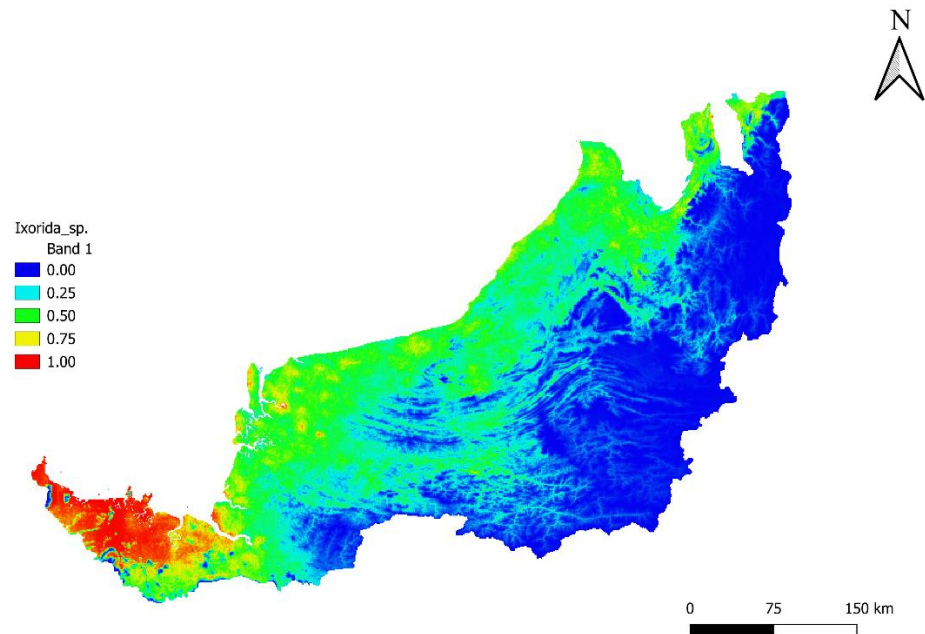


Figure 5.1: Predictive distribution map for Cetoniinae: *Ixorida* sp. in Sarawak

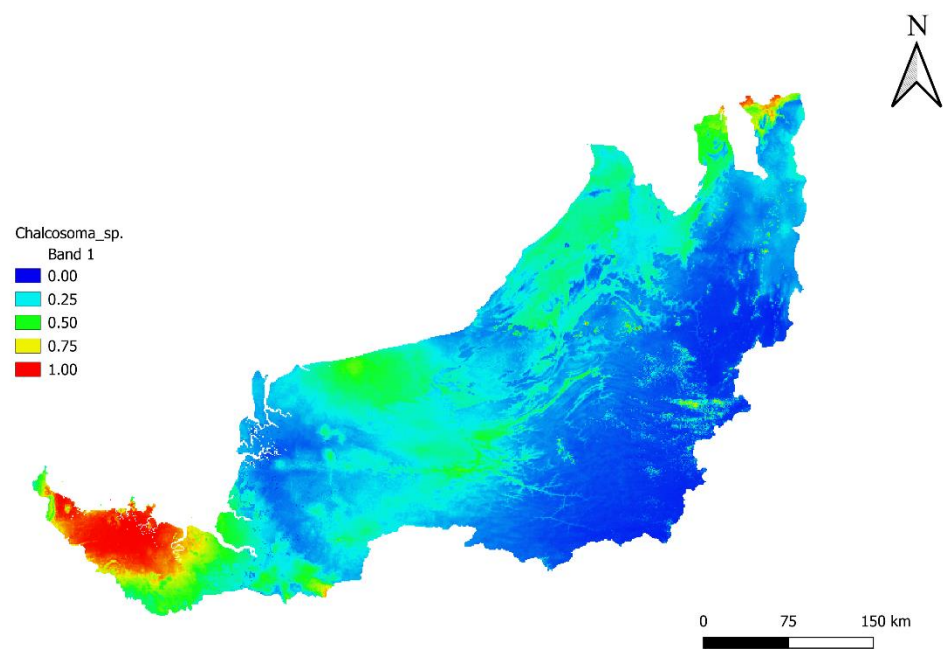


Figure 5.2: Predictive distribution map for Dynastinae: *Chalcosoma* spp. in Sarawak

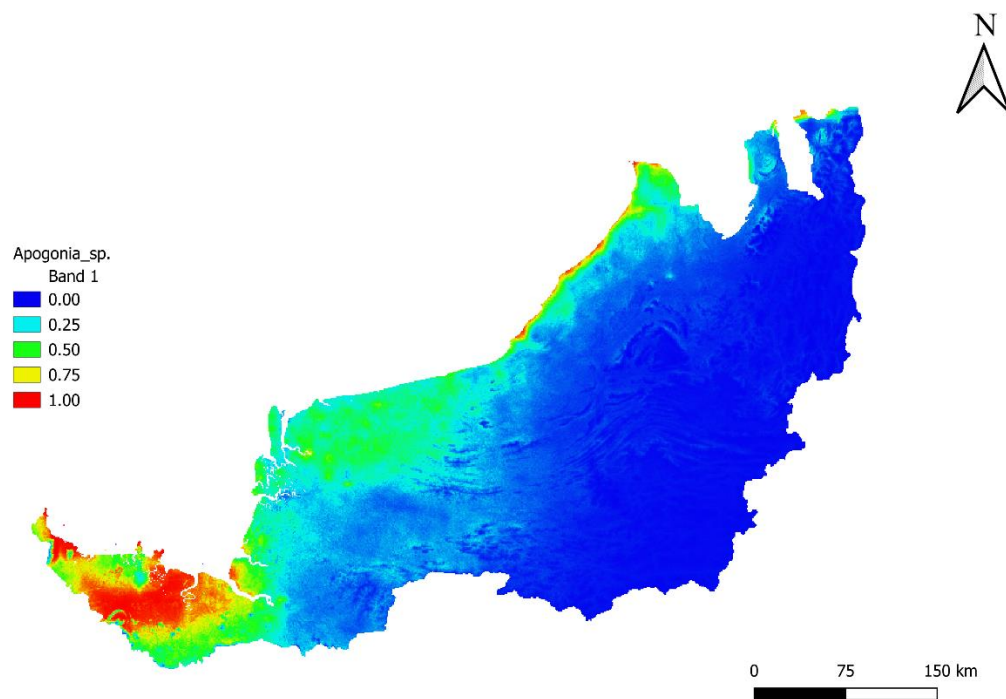


Figure 5.3: Predictive distribution map for Melolonthinae: *Apogonia* spp. in Sarawak

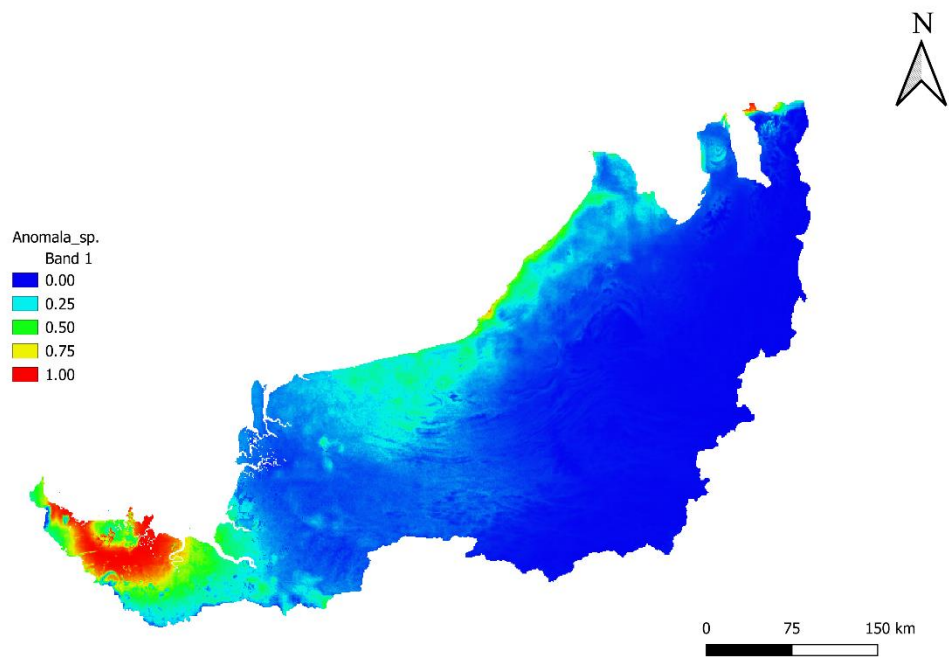


Figure 5.4: Predictive distribution map for Rutelinae: *Anomala* spp. in Sarawak

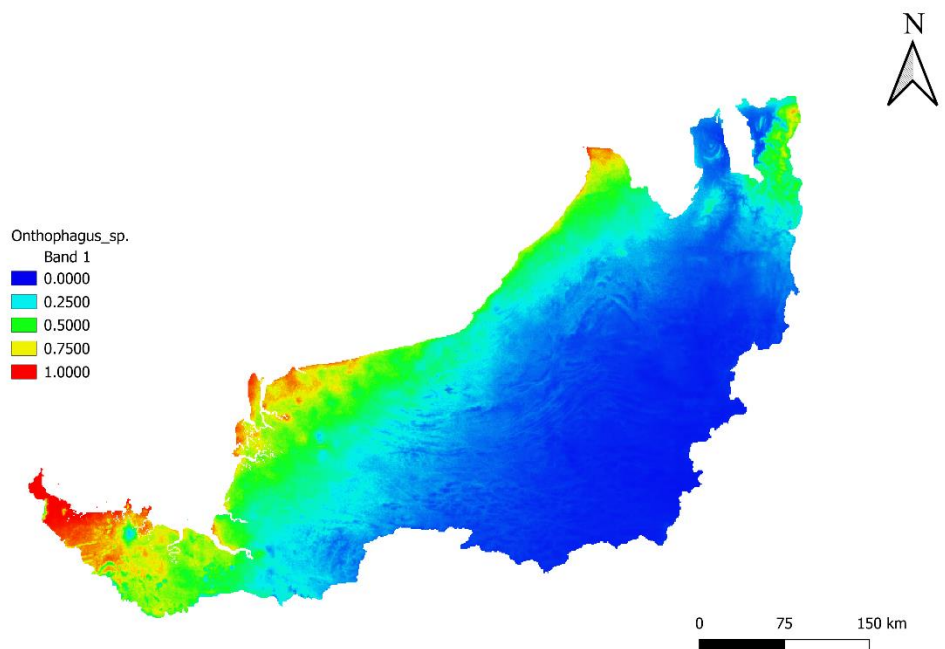


Figure 5.5: Predictive distribution map for Scarabaeinae: *Onthophagus* spp. in Sarawak

MaxEnt calculated the receiver operating characteristic (ROC) curve by graphing sensitivity versus 1-specificity. The models' predictive ability was evaluated using the area under the curve (AUC) for the ROC plot, with a value of 0.5 indicating random prediction. Table 5.3 lists the AUC values for all five examined morpho species.

Table 5.3: A list of AUC values according to receiver operating characteristic (ROC) curve plot for Scarabaeidae

Subfamilies (Morphospecies)	AUC value
Cetoniinae (<i>Ixorida</i> sp.)	0.854
Dynastinae (<i>Chalcosoma</i> spp.)	0.851
Melolonthinae (<i>Apogonia</i> spp.)	0.906
Rutelinae (<i>Anomala</i> spp.)	0.901
Scarabaeinae (<i>Onthophagus</i> spp.)	0.870

Figures 5.6 to 5.10 illustrate the receiver operating characteristic (ROC) curve plots. The relatively high AUC value performance indicated its usefulness in forecasting, as improved predictive ability was demonstrated, resulting in sensitivity and specificity values that were far superior to random (Phillips, 2006).

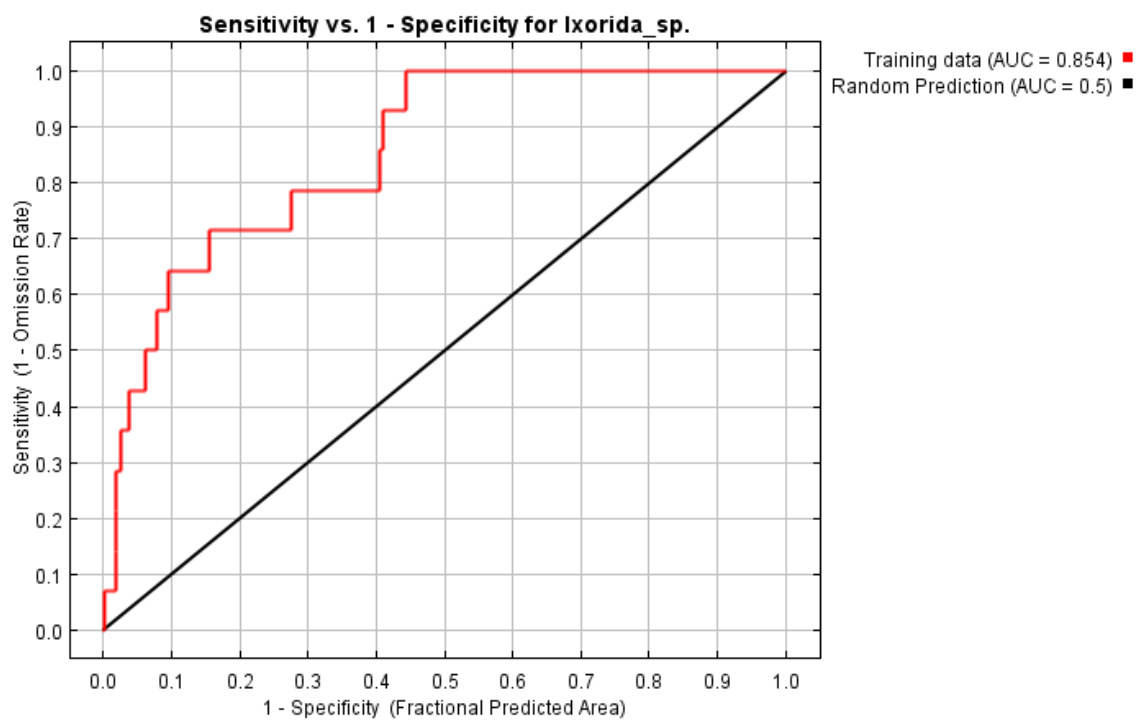


Figure 5.6: Receiver operating characteristics (ROC) curve plot for Cetoniinae: *Ixorida* spp. model

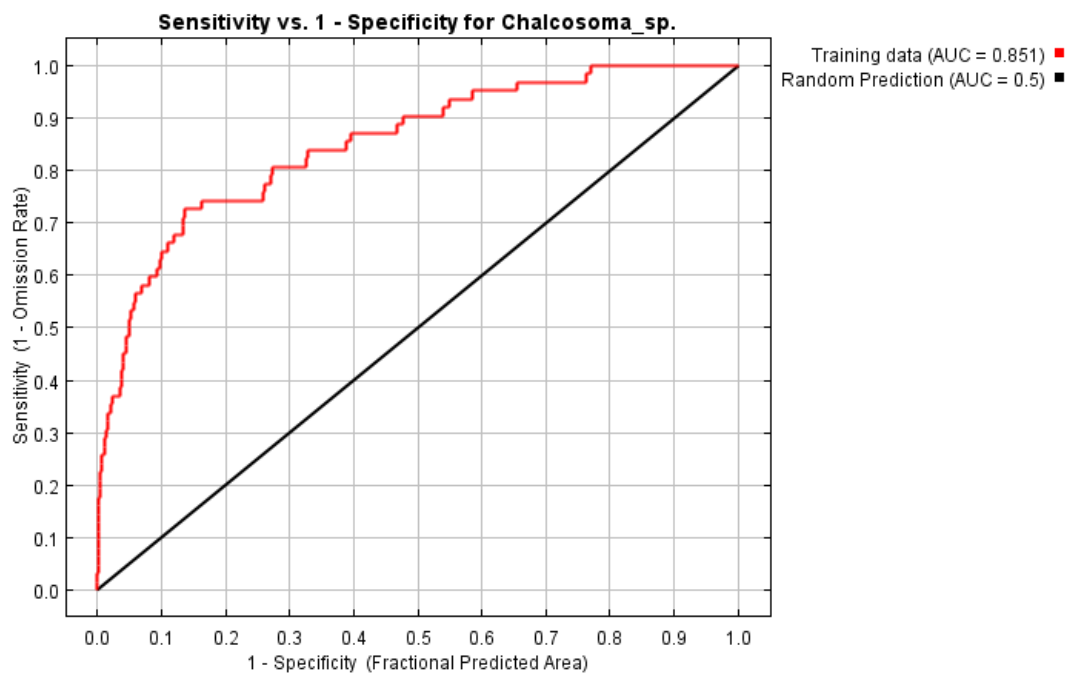


Figure 5.7: Receiver operating characteristics (ROC) curve plot for Dynastinae: *Chalcosoma* spp. model

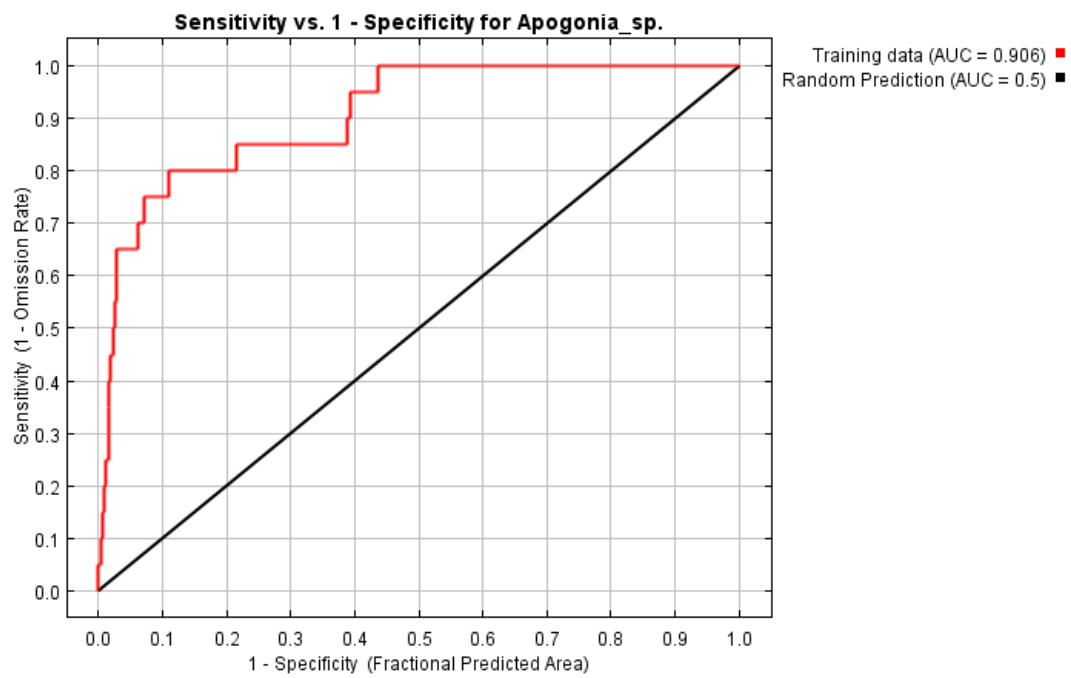


Figure 5.8: Receiver operating characteristics (ROC) curve plot for Melolonthinae: *Apogonia* spp. model

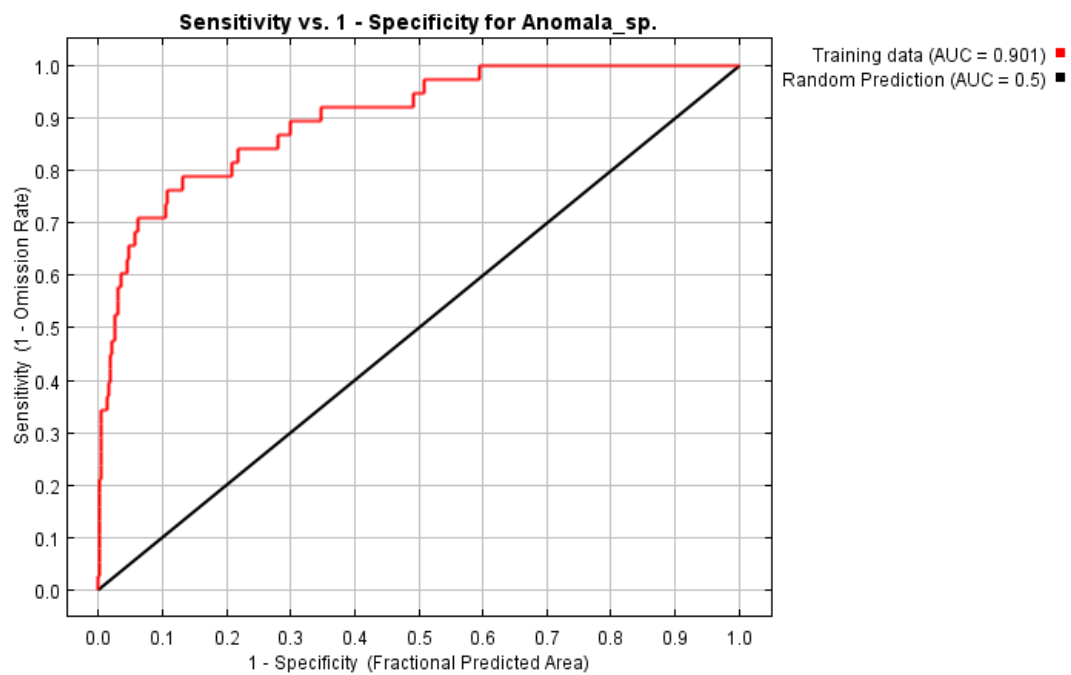


Figure 5.9: Receiver operating characteristics (ROC) curve plot for Rutelinae: *Anomala* spp. model

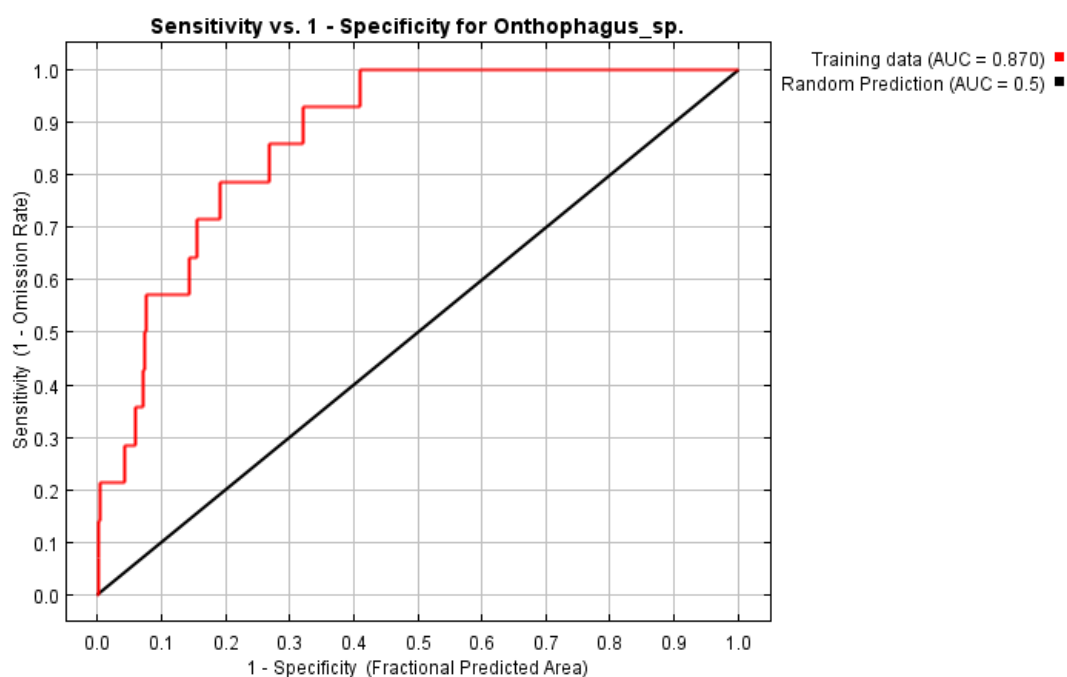


Figure 5.10: Receiver operating characteristics (ROC) curve plot for Scarabaeinae: *Onthophagus* spp. model

The important variables for each model can be determined by the increase in gain in the models provided by each variable (Baldwin, 2009; Phillips et al., 2009). All 19 variables were used in this study, but different variables contributed differently to each model (Table 5.4).

Table 5.4: Top 3 relative contributions for tested species

Subfamily (Species)	No. of variables used	Relative abundance of environmental variables (%)		
		Top 1	Top 2	Top 3
Cetoniinae (<i>Ixorida</i> sp.)	12	Bio 4 (31.6)	Bio13 (21.9)	Bio15 (8.6)
Dynastinae (<i>Chalcosoma</i> sp.)	15	Bio13 (56)	Bio15 (20.9)	Bio18 (11.4)
Melolonthinae (<i>Apogonia</i> sp.)	9	Bio15 (66.4)	Bio4 (22.7)	Bio18 (3.9)
Rutelinae (<i>Anomala</i> sp.)	14	Bio15 (47.6)	Bio13 (23.2)	Bio18 (8.4)
Scarabaeinae (<i>Onthophagus</i> sp.)	7	Bio15 (44.2)	Bio17 (36.5)	Bio18 (7.1)

For *Ixorida* sp. model from Cetoniinae, 12 variables were contributed to the predictive model, and temperature seasonality (Bio4) was recorded as the highest influencing variable with 31.6% contribution followed by precipitation of wettest month (Bio13) and precipitation seasonality (Bio15) with 21.9% and 8.9% contributions, respectively. Precipitation of the wettest month, precipitation seasonality, and precipitation of the warmest quarter were the top three contributors for *Chalcosoma* spp. model from Dynastinae with proportional weights of 56%, 20.9%, and 11.4% from 15 contributing variables. Then, nine variables contributed to *Apogonia* spp. model from Melolonthinae and Bio15 (66.4%), Bio4 (22.7%), and Bio18 (3.9%) which indicated precipitation seasonality, temperature seasonality, and precipitation of the warmest quarter as the highest contributed variables for the respective model. The *Anomala* spp. model from Rutelinae and the *Onthophagus* spp. model from Scarabaeinae had 14 and seven variables contributed to the models, respectively. Precipitation seasonality (Bio15) (47.6%), precipitation of the wettest month (Bio13) (23.2%), and precipitation of the warmest quarter (Bio18) (8.4%) were the top three contributors to *Anomala* spp. model. Meanwhile in *Onthophagus* spp. model, the three variables with highest contribution were precipitation seasonality (Bio15), precipitation of the driest quarter (Bio17), and precipitation of the warmest quarter with proportional weights of 44.2%, 36.5%, and 7.1%. (Figures 5.11-5.15).

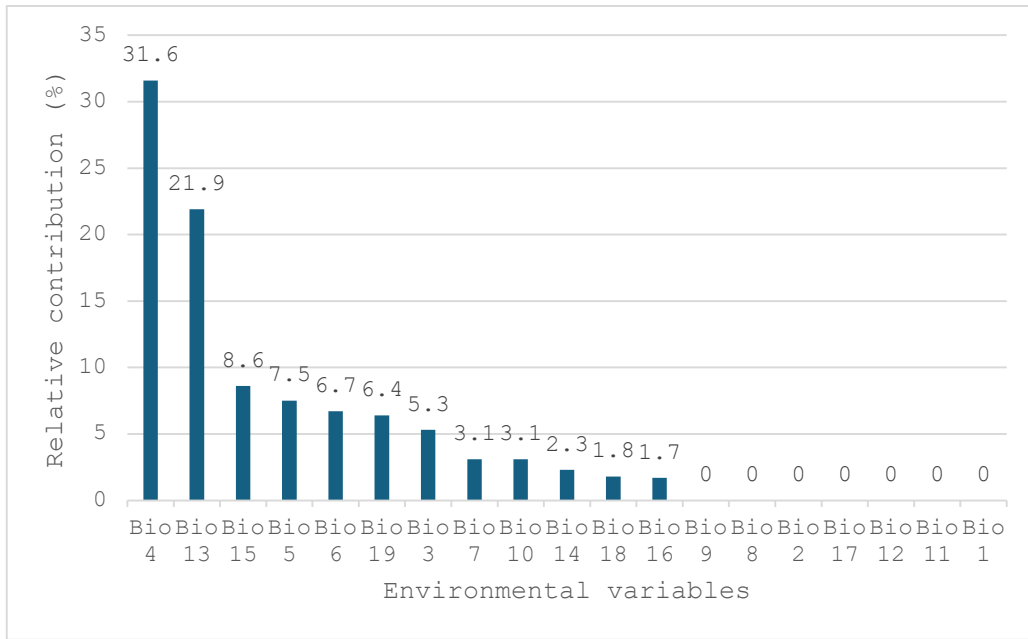


Figure 5.11: Relative contribution of the environmental variables for Cetoniinae: *Ixorida* sp.

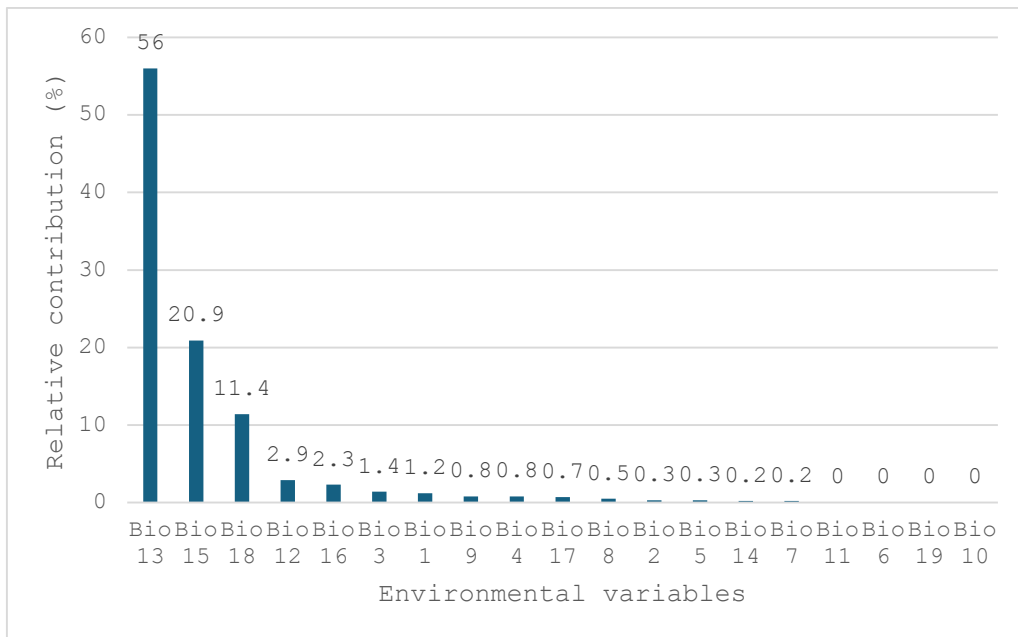


Figure 5.12: Relative contribution of the environmental variables for Dynastinae: *Chalcosoma* spp.

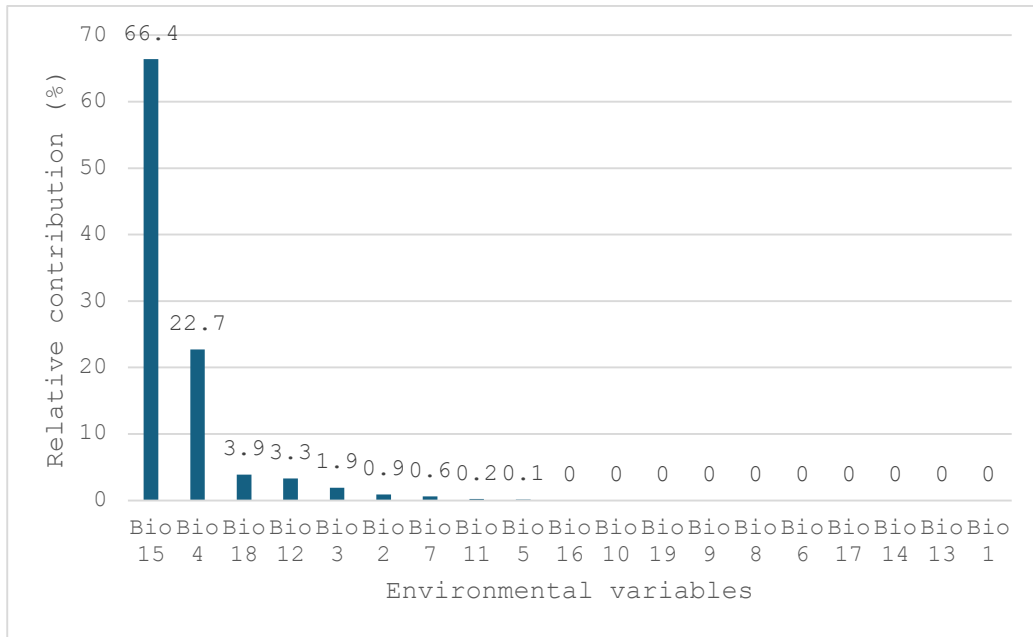


Figure 5.13: Relative contribution of the environmental variables for Melolonthinae: *Apogonia* spp.

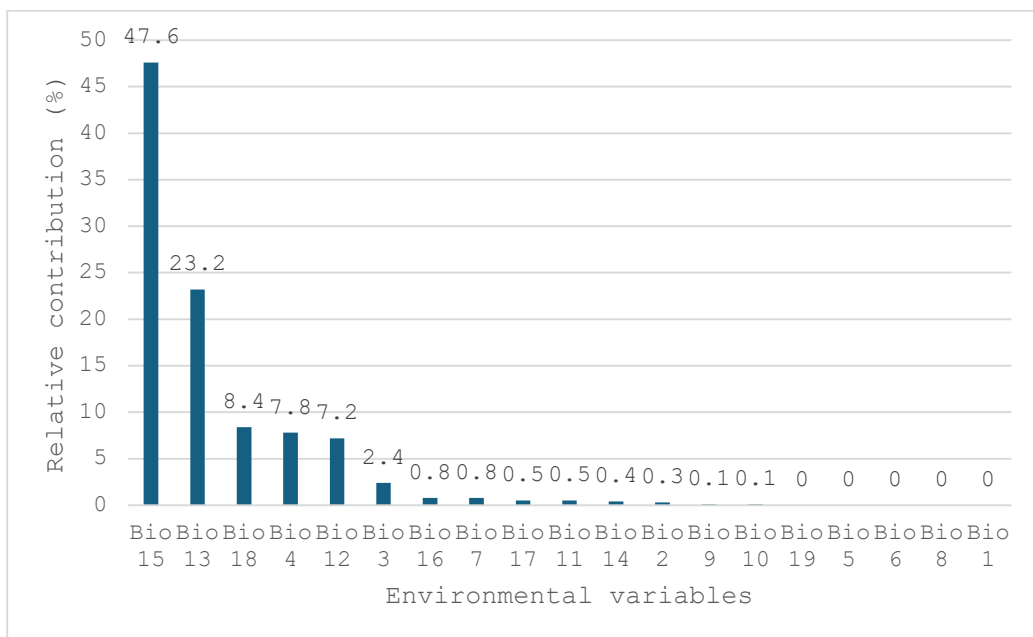


Figure 5.14: Relative contribution of the environmental variables for Rutelinae: *Anomala* spp.

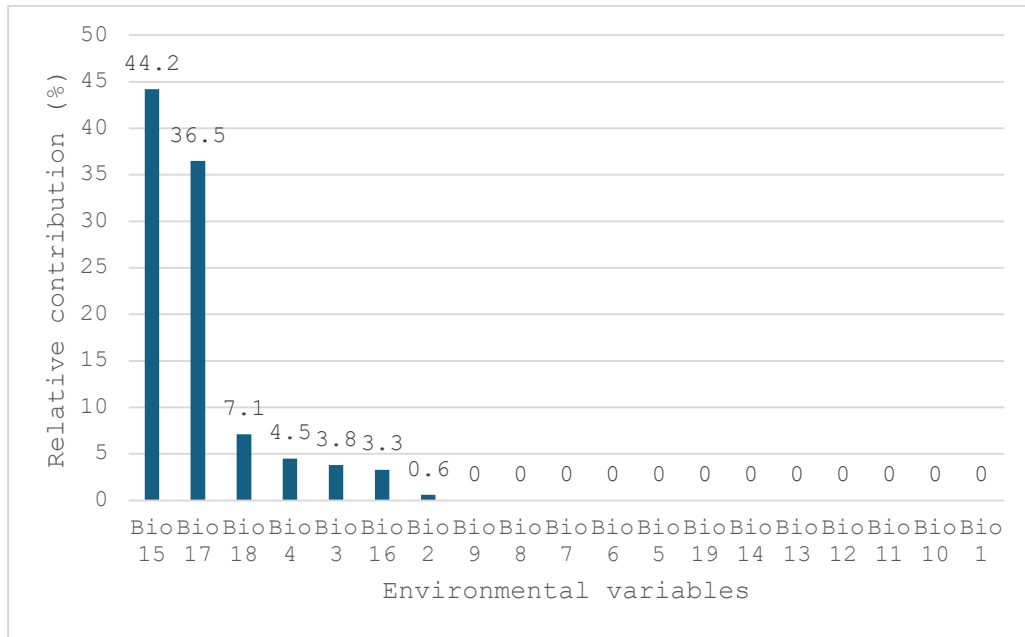
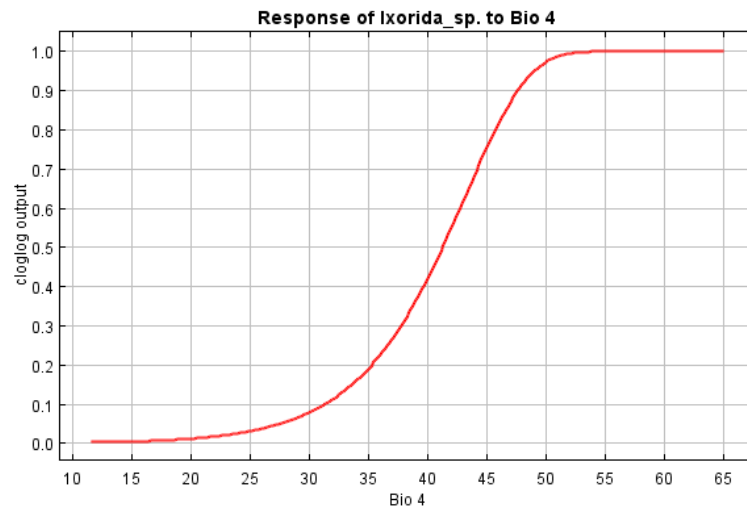


Figure 5.15: Relative contribution of the environmental variables for Scarabaeinae: *Onthophagus* spp.

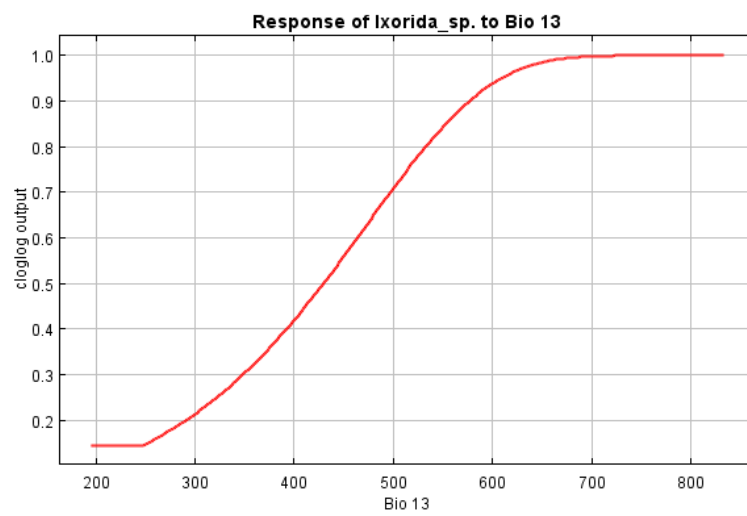
According to figures 5.16 to 5.20, the response curves of the top three contributors of each morphospecies showed how the environmental variables affecting the probability of occurrence varied. Figure 5.16 shows that the probability of occurrence of *Ixorida* sp. was highly varied with the difference between minimum and maximum temperature throughout a given year. The occurrence rate of *Ixorida* sp. was increasing rapidly as the amplitude between the highest and lowest temperatures increased. Response curves in Bio13 and Bio15 also indicated that *Ixorida* sp. had a higher occurrence rate as precipitation of the wettest month and precipitation seasonality increased.

The occurrence rate of *Chalcosoma* spp. showed an inclination as the precipitation of the wettest month (Bio13) and precipitation seasonality (Bio15) increased. This indicated that the *Chalcosoma* spp. had a higher occurrence rate during the rainy season with the highest humidity month. Besides that, response curves of Bio15 and Bio4 in *Apogonia* spp. model indicate that the distribution of *Apogonia* spp. was increasing following the temperature and precipitation seasonality. In addition, the model of *Anomala* spp. from Rutelinae showed a preference like *Chalcosoma* spp. towards the wettest month with high precipitation and high precipitation seasonality represented by Bio13 and Bio15. In the *Onthophagus* spp. model, the occurrence rate had reached the asymptote as precipitation seasonality exceeded 60 mm. On the other hand, the occurrence rate underwent declination, inversed with the precipitation of the driest quarter. However, there were declinations in the occurrence rate of *Chalcosoma* spp., *Apogonia* spp., *Anomala* spp., and *Onthophagus* spp. when responding to Bio18, the precipitation of the warmest quarter. While reversely varied to Bio18, small rebounds appeared in all models above except the model of *Onthophagus* spp., around 600 to 700 mm for *Chalcsosma* spp., and within 500 to 700 mm in both models of *Apogonia* spp. and *Anomala* spp. precipitation in the warmest quarter (Bio18).

a)



b)



c)

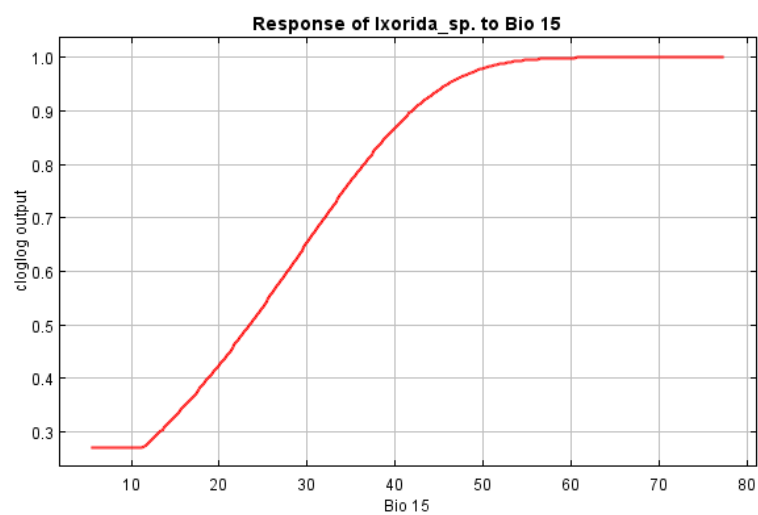
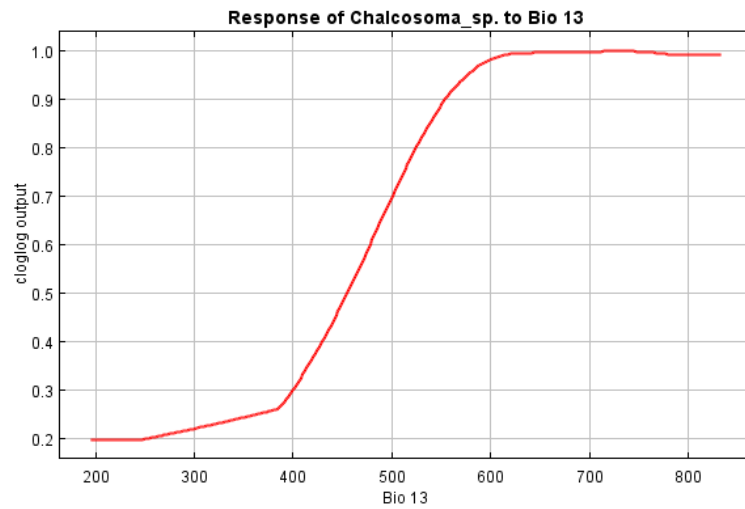
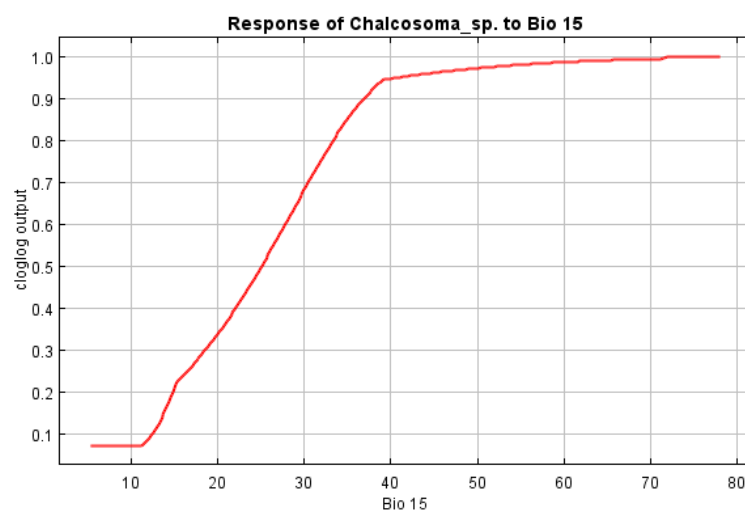


Figure 5.16: Response curves of the top three predictor variables with the greatest percent of contribution for *Cetoniinae*: *Ixorida* sp. a) Bio4, b) Bio13, and c) Bio15

a)



b)



c)

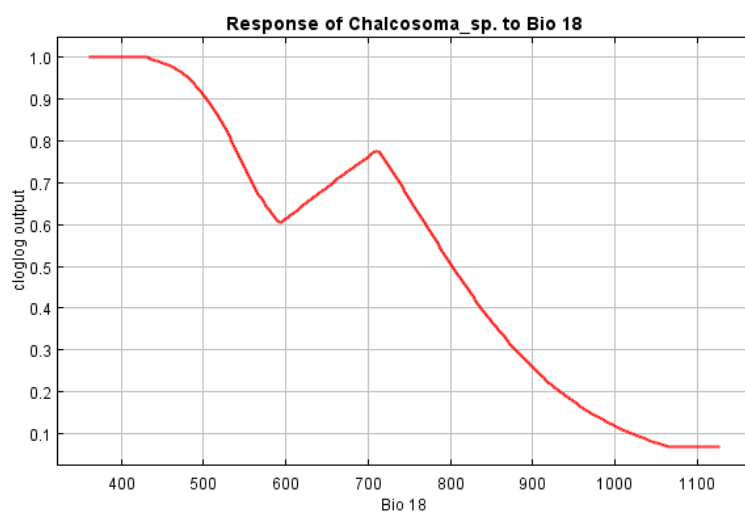
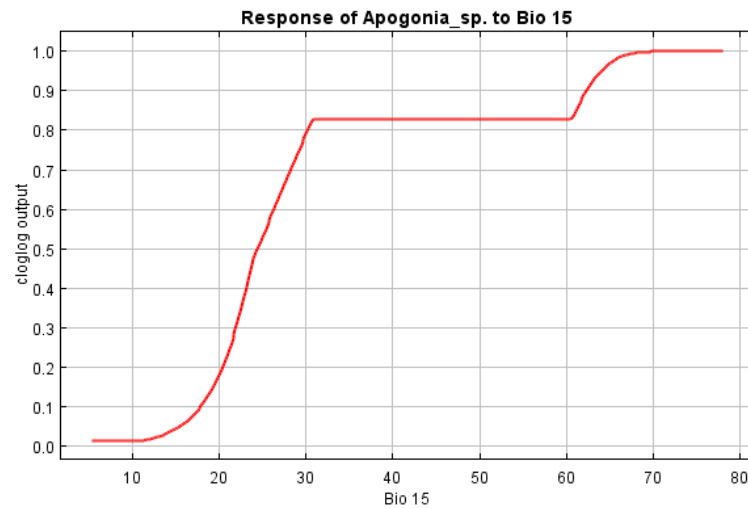
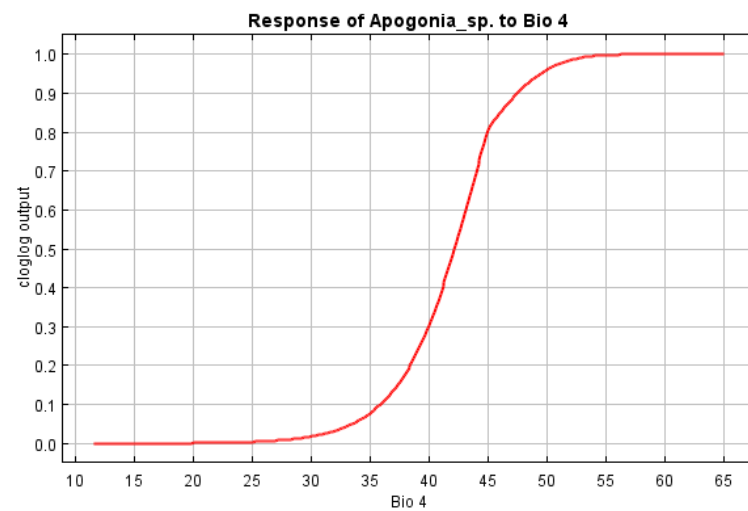


Figure 5.17: Response curves of the top three predictor variables with the greatest percent of contribution for Dynastinae: *Chalcosoma* sp. a) Bio13, b) Bio15, and c) Bio18

a)



b)



c)

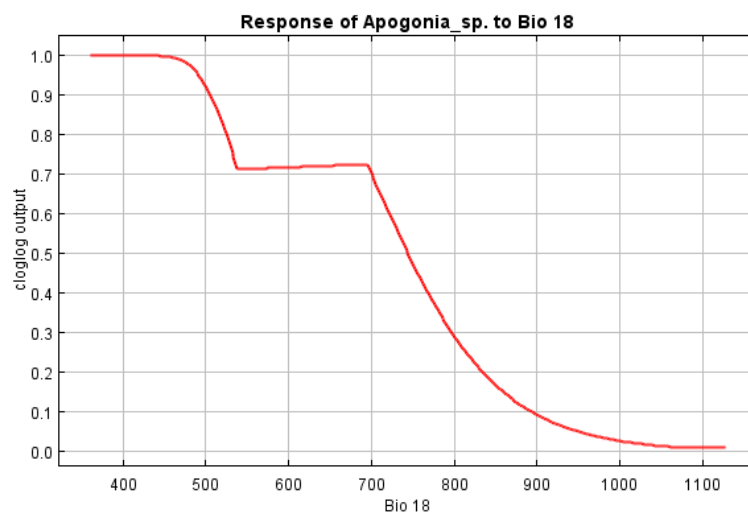
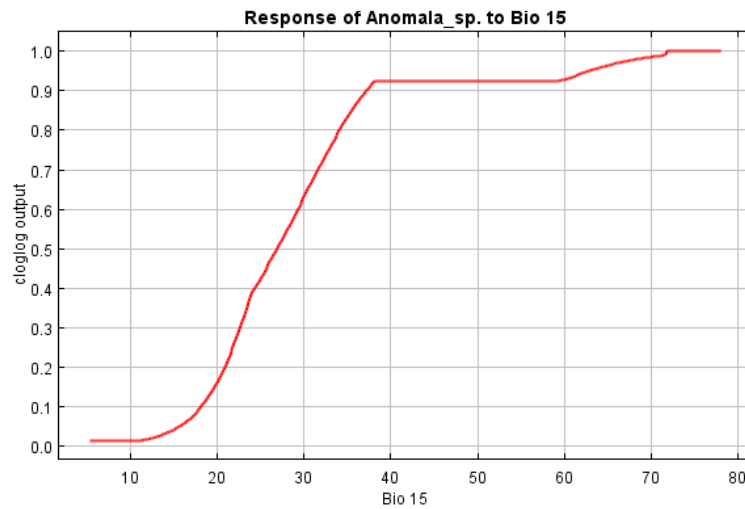
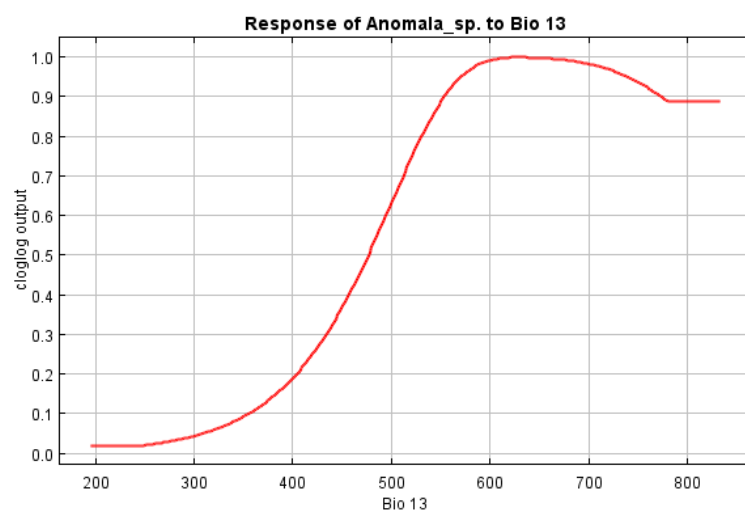


Figure 5.18: Response curves of the top three predictor variables with the greatest percent of contribution for Melolonthinae: *Apogonia* sp. a) Bio15, b) Bio4, and c) Bio18

a)



b)



c)

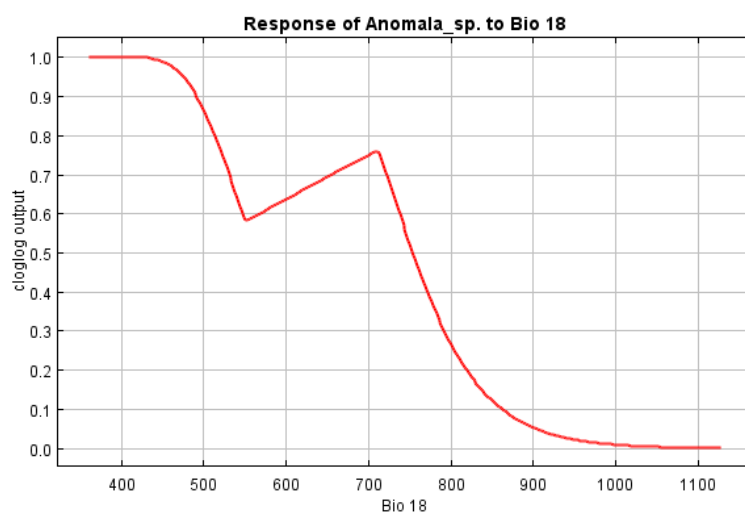
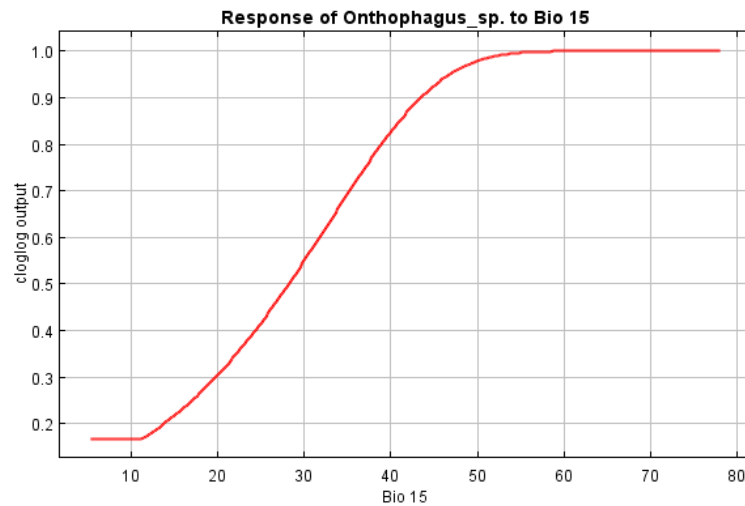
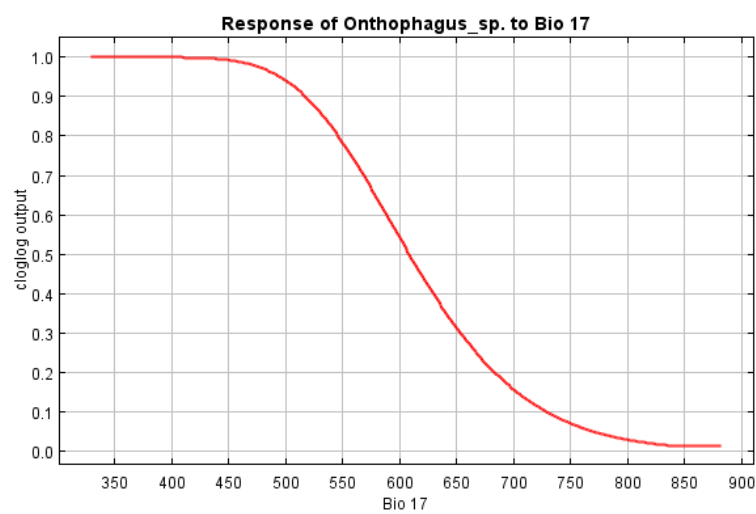


Figure 5.19: Response curves of the top three predictor variables with the greatest percent of contribution for Rutelinae: *Anomala* sp. a) Bio15, b) Bio13, and c) Bio18

a)



b)



c)

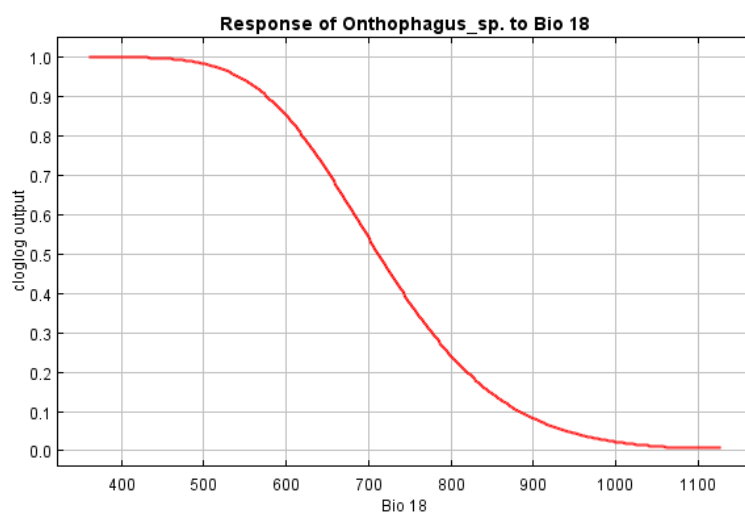


Figure 5.20: Response curves of the top three predictor variables with the greatest percent of contribution for Scarabaeinae: *Onthophagus* sp. a) Bio15, b) Bio17, and c) Bio18

On the other hand, a jackknife test provides an alternate estimate for assessing variable importance (Yost et al., 2008; Phillips et al., 2009) where it created the models by using the variable in isolation (Table 5.5).

Table 5.5: Jackknife test of variable importance in the MaxEnt model

Model	Highest gain when isolated	Lowest gain when omitted
Cetoniinae: <i>Ixorida</i> sp.	Bio4	Bio4
Dynastinae: <i>Chalcosoma</i> spp.	Bio13	Bio18
Melolonthinae: <i>Apogonia</i> spp.	Bio4	Bio12
Rutelinae: <i>Anomala</i> spp.	Bio4	Bio12
Scarabaeinae: <i>Onthophagus</i> spp.	Bio17	Bio17

For the *Ixorida* sp. model, Bio4 was determined to give the most information by itself as Bio4 had the highest gain when used in isolation. However, at the same time, Bio4 also decreased the gain the most in the *Ixorida* sp. model when it was omitted. Then, Bio13 had the highest gain in the *Chalcosoma* spp. model when isolated, while Bio18 was the important environmental variable that would decrease the gain the greatest if isolated. In both *Apogonia* spp. and *Anomala* spp. models, Bio4 was the highest scorer in their jackknife tests. However, the environmental variable that decreased the most when excluded in both models was Bio12, indicating that Bio12 carried the largest amount of information absent in other variables. Like the *Ixorida* sp. model, the *Onthophagus* spp. model had the same environmental variable that gave out the most useful information by itself and decreased the gain the most when omitted which was Bio17 (Figures 5.20-5.25).

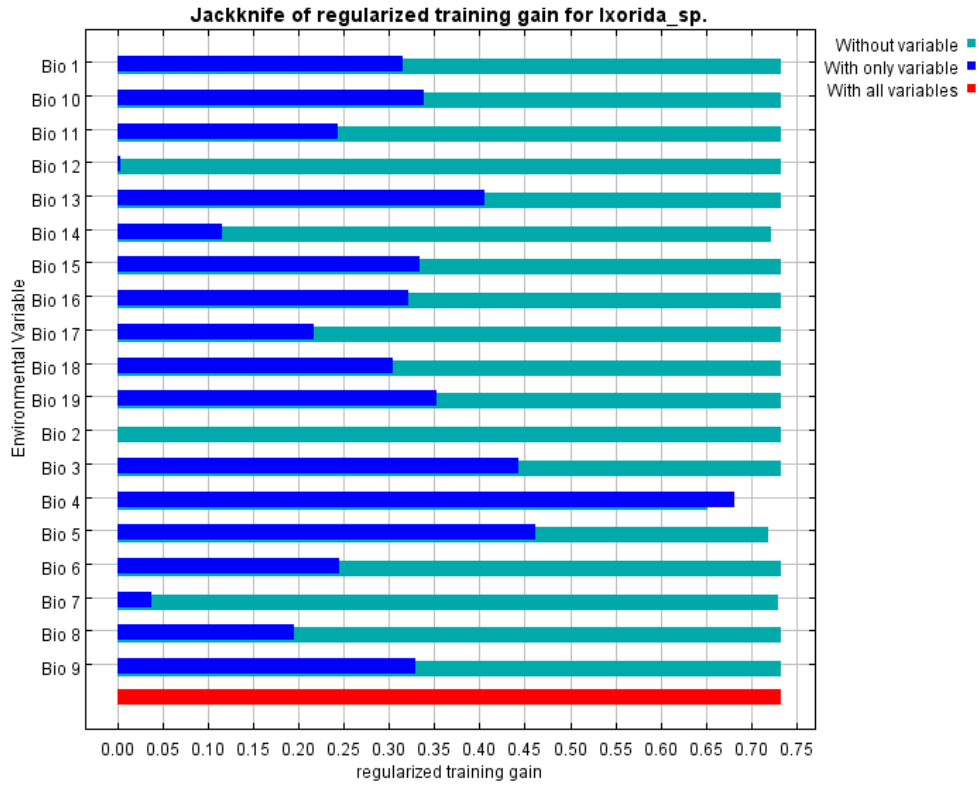


Figure 5.21: Jackknife test of variable importance in the MaxEnt model of Cetoniinae: *Ixorida* sp.

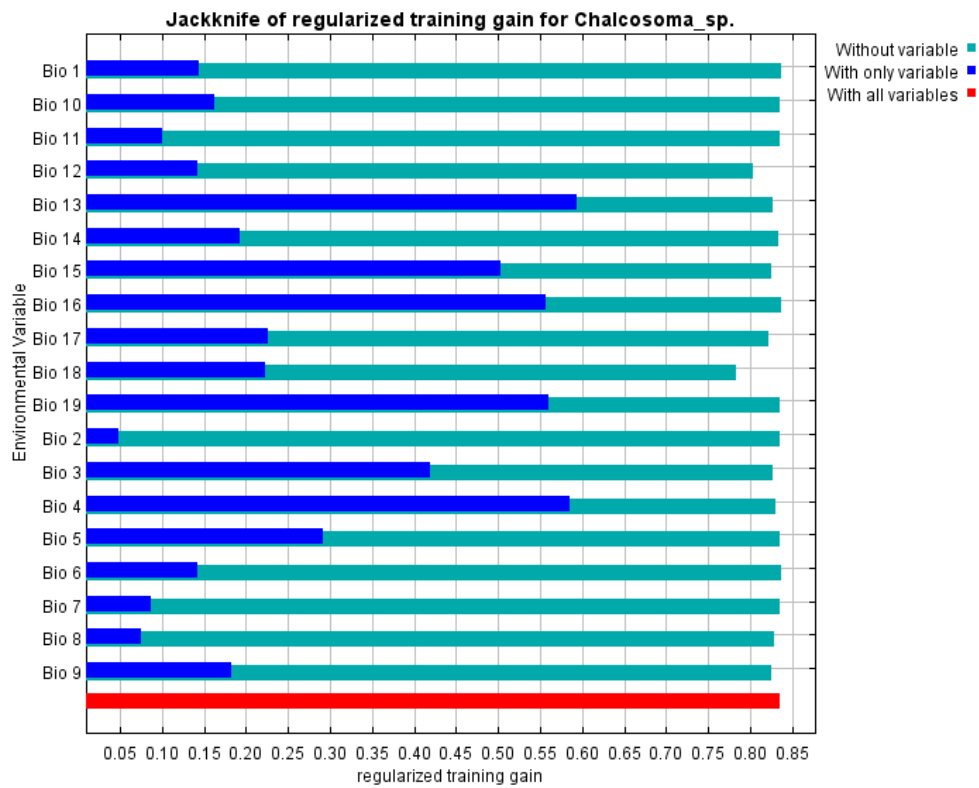


Figure 5.22: Jackknife test of variable importance in the MaxEnt model of Dynastinae: *Chalcosoma* spp.

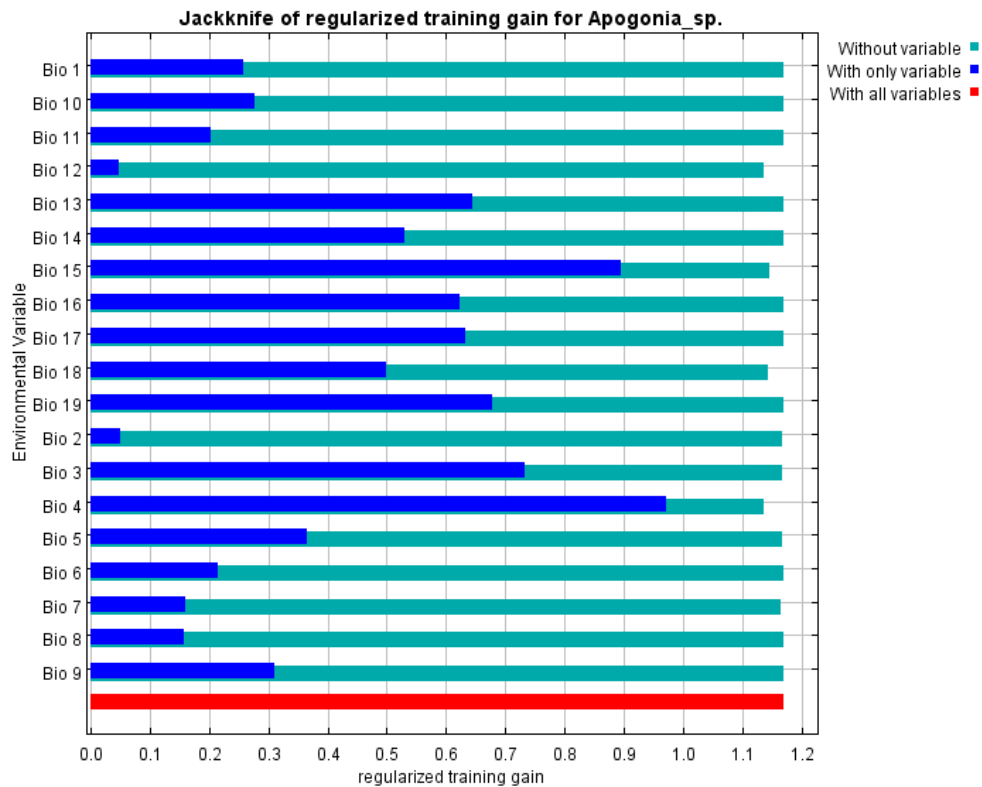


Figure 5.23: Jackknife test of variable importance in the MaxEnt model of Melolonthinae: *Apogonia* spp.

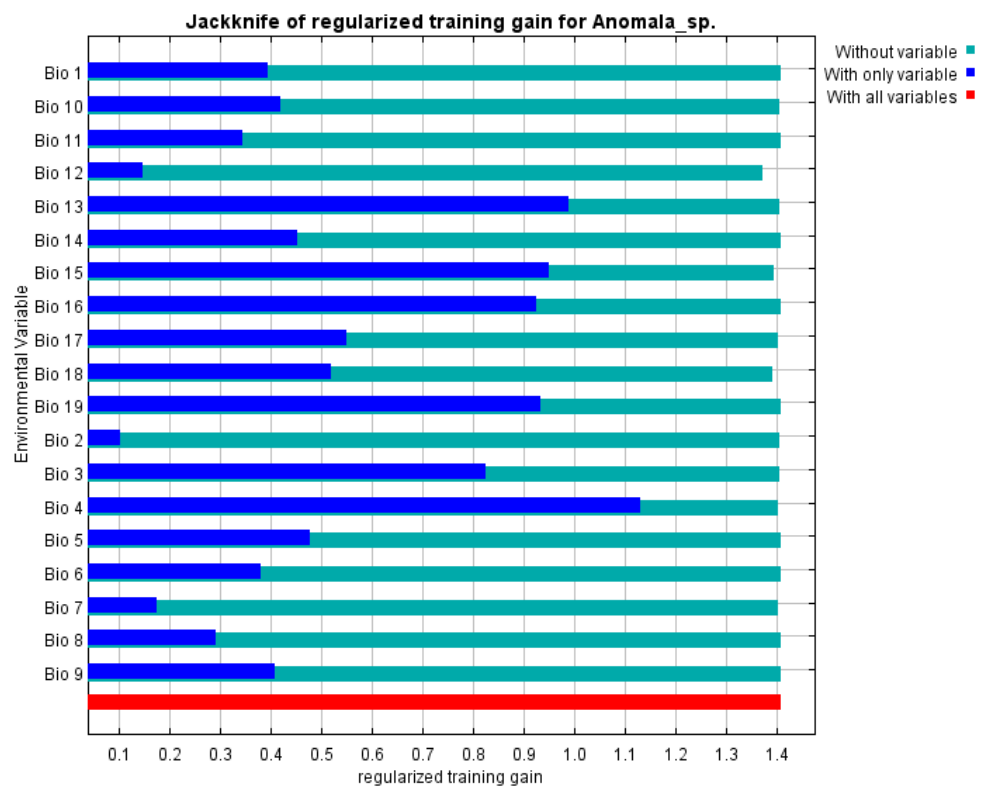


Figure 5.24: Jackknife test of variable importance in the MaxEnt model of Rutelinae: *Anomala* spp.

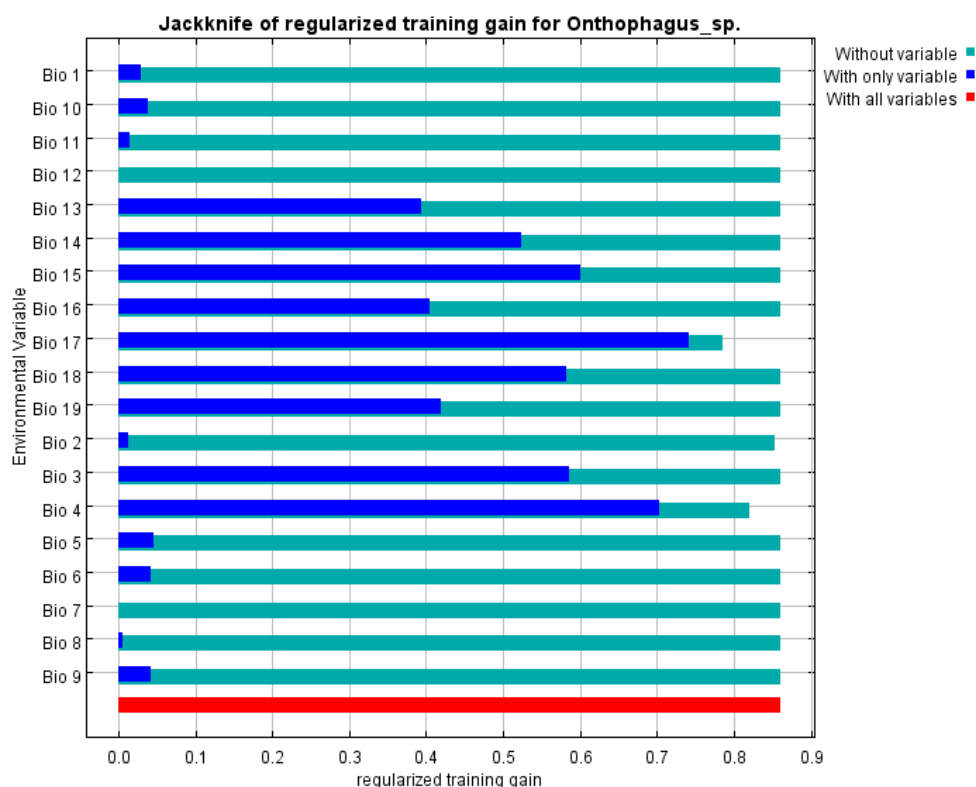


Figure 5.25: Jackknife test of variable importance in the MaxEnt model of Scarabaeinae: *Onthophagus* spp.

5.4 Discussion

The spatial distribution modelling is an important tool for conservation planning by conservationists due to its capability to predict the potential of a population to occupy an area without field or biological surveys (Corsi et al., 2000; Loiselle et al., 2003). Hence, the biophysical environment requirements for certain populations can be provided through spatial distribution modelling associated with the occurrence records. The scarcity of occurrence data is always a common problem in modelling. The accuracy or reliability of the predictive model varies conversely to the occurrence data provided in terms of sample size, locality accuracy, and identification level. In this study, although geographic coordinates and identification details were provided or accessed through various sources, most of the information provided was limited with low accuracy. For example, many

occurrence data were recorded until genus level instead of species level, *Apogonia* sp. was recorded to represent unidentified individuals instead of *Apogonia destructor*, *A. waterstradti*, or *A. expeditionis*. Meanwhile, some of the geographic coordinates provided are inadequate like Kota Samarahan was recorded instead of UNIMAS, Kota Samarahan in detailed (Stockwell & Peterson, 2002; Pearson et al., 2007; Elith & Leathwick, 2009). Thus, the reliability of the models generated will always be questioned due to limited data as some researchers agreed that the accuracy of models increases conversely with the sample sizes and is influenced by the taxonomic rank used (Pearce & Ferrier, 2000; Hernandez et al., 2006; Millar et al., 2017). However, although the genus rank of Scarabaeidae was chosen instead of species level in the spatial distribution modelling due to limited information, the models are useful to provide an overall view of the spatial distribution maps for all Scarabaeidae genera throughout the Sarawak landscape.

Besides ecological and evolutionary history, exposure to diverse abiotic and biotic conditions, resource availability, nutritional ecology, and sometimes sex will also contribute to Scarabaeidae's distribution or population dynamics (Appleman, 1979; Facundo et al., 1999; Cohen, 2004; Schowalter, 2011). With the association of spatial distribution modelling, the potential distribution area of Scarabaeidae can be predicted which is highly concerned and economically important for human like decomposers, agricultural pests, pollinators, and others. The burrowing activity of dung beetles is important in transporting minerals back into the soil considering them as keystone species that bring ecological importance to certain areas, for example, pasture ecosystems with tons of animal dungs (Pal, 2003; Ravan, 2003). According to Facundo et al. (1999), different sexes of beetle from similar species have different emergence data as they don't share the same behaviours and spatial distribution concerning vegetation types. For example, *Chalcosoma* spp. will mostly gather at hidden or high food spots to compete for

food sources or mating opportunities, and the females of *Chalcosoma* spp. will relocate onto the ground or underground to lay their eggs while the males will search for other spots further from the previous spot. Therefore, sometimes the occurrence data differs according to sex and the collecting methods.

The animal-plant association relationship doubtlessly is one of the major variables manipulating the outcome of spatial distribution data (Johnson & Scriber, 1994). Schowalter (2011) stated that the reproduction or seed allocation of plants is affected by herbivore insects in direct and indirect ways. Especially in plants that highly depend on pollinators in reproduction and dispersion in tropical regions, certain plants may disappear from certain areas if their pollinators become rare or extinct (Powell & Powell, 1987). Some plants even possess the ability to emit carrion odours to attract saprophagous beetles like dung beetles to associate with pollination (Appanah, 1990; Norman et al., 1992).

From the results, all models showed a distribution trend toward the western part of Sarawak. This is potentially due to many areas in Betong and Sri Aman Divisions that had been developed into plantations areas comprising of rubber (*Hevea brasiliensis*), cocoa (*Theobroma cacao*), pepper (*Piper nigrum*), enau (*Arenga pinnata*) and oil palm following agreements between the Native and Sarawak Land Development Board (SLDB) and the Sarawak Land Consolidation and Development Authority (SALCRA) (Mertz & Christensen, 1997; Sanggin & Mersat, 2012). Although there was no record of the pollination ecology of the *Ixorida* genus in Sarawak, there were studies that discussed the pollination effectiveness of flower chafer genera including *Protaetia*, *Eucetonia*, *Leucocelis*, and others in *Eulophia* spp. (Orchidaceae) and *Magnolia* spp. (Magnoliaceae) (Matsuki et al., 2008; Peter & Johnson, 2009). In the case of *Chalcosoma* and *Apogonia*

genera, they are notorious for their damage to oil palms especially *C. atlas* (Pradana, 2020; Kalidas & Subbanna, 2022) and distributed wider after oil palm plantation had reached around 1.62 million hectares within Sarawak at 2023 (Siddharta, 2024). According to Goh et al. (2016), they stated that the tropical rainforest region is preferred by oil palms which also indicates the suitability of oil palms in Malaysia together with growth of both *Chalcosoma* and *Apogonia* genera. The genus *Anomala* was found as a common but important pest in Malaysia (Hill, 2008) which may cause up to 20% rise in mortality rate by attacking all parts of the trees during adult and larval stages as forest tree defoliators and nursery stocks pest every generation (Bandara, 1990; Wylie & Spelight, 2012). In Sarawak, the most used anthelmintic is ivermectin for deworming buffaloes. The pesticide content might be one of the affections of *Onthophagus* spp. distribution in Sarawak (Harizt et al., 2021) as the ivermectin will inhibit the development and growth of scarab beetles.

In this study, the results show that MaxEnt exhibits a high computational efficiency and produces an extensive statistical report of the model since ecologists have been intrigued by the factors that affect the geographic distributions of the population over two centuries (Schowalter, 2011). The results have shown the influence of environmental variables on the distribution of Scarabaeidae. Bio15, precipitation seasonality was the top contributor for all the tested genera except for Cetoniinae, *Ixorida* sp. and this result might be a consequence of the smallest sample size of *Ixorida* sp. was collected and recorded in this research due to limited accessibility of data. In tropical rainforests, precipitation seasonality is an important variable in spatial distribution modelling because the precipitation will affect the decomposition of dead plant structure above the forest ground while also affecting the distribution of Scarabaeidae when the

acidity of the soil layer is affected. The soil organic carbon (SOC) in forests or certain areas responds to precipitation patterns according to climate change globally, including the quantity, intensity, and frequency of precipitation events (Kirchmeier-Young & Zhang, 2020). Other than the SOC, the precipitation patterns also alternate the soil physiochemical and biological properties. For example, the temperature of soil, nitrogen content, and the activities of microbial communities affecting the development of flora communities which are food sources for some species of scarab beetles during grub stages (Chen et al., 2019; Xu et al., 2024). A study conducted by Venkateswaran et al. (2022) suggested that the grub population is affected by the precipitation and the moisture of substrate. This is because *Holotrichia serrata* from Melolonthinae having a positive association to bulk density while negative association to soil porosity with precipitation as one of the factors. On the other hand, both parameters showed a negative association with *Adoretus* sp. from Rutelinae. Additionally, positive and negative correlation between pH value and *H. serrata* and *Adoretus* sp. were concluded, respectively (Venkateswaran et al., 2022). In China, a research conducted by Shang et al. (2022) mentioned that *Alissonotum impressicolle* from Dynastinae was found to be more attracted to soils with neutral or slightly acidic properties and abundant organic matter. Thus, the precipitation seasonality can be one of the important environmental variables that affected the spatial distribution models for selected genera.

5.5 Conclusion

In this chapter, the effectiveness of spatial distribution modelling in conservation planning using scarab beetle's responses to environmental conditions is presented. Even though the accuracy might be challenged due to the limited number of occurrences, and geographical sampling biases, this models still show evidence of how the population

disperses across the landscape of Sarawak. It is recommended that the efficiency of data collection and documentation should be practiced providing more concreted occurrence data for further spatial distribution assessment conducted.

CHAPTER 6

GENERAL SUMMARY AND CONCLUSION

This research has increased our knowledge of how the diversity and spatial distribution of Scarabaeidae are influenced by environmental conditions and variables. Additionally, an overview of the Scarabaeidae checklist from Sarawak indicates the impact of various human activities. For example, Sabal Agroforestry and Kampung Serpan Laut were found as the localities with the highest and lowest species diversity, respectively, in this research. Human disturbances such as anthropogenic activities, agricultural activity, tourism, and others are always factors that affect biodiversity which requires conservation concerns.

Chapter 4 shows that Scarabaeidae diversity according to localities and forest types is undeniably related to biotic and abiotic factors. Some Scarabaeidae species require good living conditions throughout their life cycles, especially during the egg and grub stages as they are highly reliable to the substrate conditions such as acidity, ventilation, humidity, and others. Different forest types also support different diversities of Scarabaeidae as they contain different flora and fauna diversities, which are influenced by the environmental conditions of each forest types. This also led to different similarities between each locality and forest type as not all Scarabaeidae species share the same characteristics or behaviours. Apart from this, the Scarabaeidae abundance and diversity are also able to contribute to conservation planning for conservationists. For example, the heath forest has high Scarabaeidae abundance but the lowest diversity while the mixed dipterocarp forest has the highest diversity. Meanwhile, the highest similarity was found between the mixed dipterocarp forest and the limestone forest, whereas the lowest similarity was found between the mixed dipterocarp forest and the mangrove forest. This

highlights how biodiversity is influenced by different localities that serve different purposes from human residential areas to forest reserves and how different forest types impact biodiversity.

The reason for how spatial distribution modelling varied as the environmental conditions and variables such as annual temperature range, precipitation of the wettest month, temperature seasonality, and others were presented in Chapter 5 which can provide more assured data for conservation planning. The environmental variables Bio 4, Bio 13, Bio 15, Bio 17, and Bio 18 representing temperature seasonality, precipitation of the wettest month, precipitation seasonality, precipitation of the driest quarter, precipitation of the warmest quarter were the top contributors to the distribution of Scarabeidae across the Sarawak region. According to the potential distribution maps presented in Chapter 5, it showed that all of the genera selected were most likely to be distributed in areas with higher latitudes. However, for *Onthophagus* sp., despite a similar distribution map to the others, the species also showed a distribution towards the coastal line in the division of Sibul, Bintulu, and Miri.

In conclusion, both diversity and spatial distribution play important roles in conservation or development planning. Studies on diversity provide first-hand data for environmental impact assessments in one place or an area as Scarabaeidae possess features in indicating environmental health. Spatial distribution modelling provides aid for conservationists to propose or plan further conservation planning according to population dispersion. Increasing the knowledge of diversity and spatial distribution provides more understanding of the distributional ecology and such information helps in conservation planning. It is also recommended that further sampling or studies in

distributional ecology be conducted for a more detailed database, which will aid in future conservation efforts.

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Appendix A

Subfamily	Species	No. of individuals																	
		G	R	K	A	M	S	G	S	S	L	L	S	G	F	G	G	N	Total
		G	L	S	B	S	A	N	m	b	B	H	W	T	C	p	R	N	
		N	L	L	R				t	k	N	N	S					P	
		P									P	P							
Cetoniinae	<i>Agestrata orichalcea</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Agestrata belitungana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	<i>Chalcothea affinis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
	<i>Ixorida regia sumatrana</i>	0	0	0	0	0	1	0	0	16	4	0	0	2	0	25	0	6	54
	<i>Protaetia</i> sp.1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Taeniodera inermis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	<i>Taeniodera monacha</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	<i>Taeniodera</i> sp.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	Cetoiinae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	3
	Cetoiinae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Cetoiinae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	5	
Aphodiinae	<i>Aphodius</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	5
	<i>Aphodius</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3
Dynastinae	<i>Chalcosoma atlas</i>	3	0	0	0	2	3	11	3	0	1	0	2	2	1	0	0	0	28

	<i>Allomyrina pfeifferi pfeifferi</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	<i>Dichodontus coronatus</i>	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4
	<i>Oryctes</i> sp.1	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	4
	<i>Oryctes gnu</i>	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
	<i>Oryctes rhinoceros</i>	0	1	2	0	0	0	0	1	2	0	0	0	0	0	4	0	1	11
	<i>Temnorhynchus baal</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
	<i>Trichogomphus lunicollis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	<i>Xylotrupes gideon</i>	0	0	0	0	0	0	0	2	1	0	2	0	0	0	0	0	0	5
	<i>Xylotrupes gideon borneensis</i>	0	0	0	0	0	2	25	0	0	0	0	0	0	1	3	0	2	33
Melolonthinae	<i>Apogonia</i> sp. 1	122	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	127
	<i>Apogonia</i> sp. 2	0	14	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	15
	<i>Apogonia</i> sp. 3	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5
	<i>Apogonia</i> sp. 4	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
	<i>Apogonia</i> sp. 5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Apogonia</i> sp. 6	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Apogonia expeditionis</i>	0	30	11	1	2	3	1	13	12	6	1	28	0	0	0	0	0	108
	<i>Apogonia destructor</i>	0	0	51	0	3	8	4	31	32	12	9	117	3	5	34	6	0	315
	<i>Apogonia palawana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	<i>Apogonia ritsemae</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1

<i>Apogonia waterstradti</i>	0	0	3	0	0	5	2	4	6	5	3	12	0	1	3	0	0	44
<i>Adoretus compressus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	1	0	5
<i>Asactopholis pectoralis</i>	0	0	0	0	0	2	0	0	10	0	0	0	0	0	0	0	1	13
<i>Catharsius</i> sp.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Exopholis</i> sp.1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Exopholis hypoleuca</i>	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	4
<i>Holotrichia</i> sp.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Holotrichia loochooana</i>	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	0	0	5
<i>Holotrichia serrata</i>	4	10	1	3	2	1	0	9	16	0	1	0	19	1	1	1	0	69
<i>Hoplia</i> sp. 1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3
<i>Hoplia</i> sp. 2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Hoplia</i> sp. 3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Hoplia</i> sp. 4	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
<i>Hoplia</i> sp. 5	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
<i>Hoplia aurata</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
<i>Lepidiota</i> sp.1	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	15
<i>Lepidiota caesia</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Lepidiota mellyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Lepidiota stigma</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2

<i>Leucopholis emarginata</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Leucopholis staudingeri</i>	10	0	0	1	0	0	2	1	2	0	0	3	2	0	0	0	0	21
<i>Maladera</i> sp. 1	3	0	0	0	0	0	0	0	6	1	3	8	1	1	1	1	0	25
<i>Maladera</i> sp. 2	7	0	0	0	0	0	0	0	4	0	0	14	0	0	0	0	0	25
<i>Maladera</i> sp. 3	0	0	1	0	2	0	0	0	2	0	0	11	0	0	0	0	0	16
<i>Maladera</i> sp. 4	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	3
<i>Maladera</i> sp. 5	0	0	0	0	0	1	0	0	14	0	0	0	0	0	0	0	0	15
<i>Maladera</i> sp. 6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Maladera</i> sp. 7	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	6
<i>Maladera</i> sp. 8	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	5
<i>Maladera</i> sp. 9	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	5
<i>Maladera castanea</i>	0	0	0	0	0	1	0	0	0	11	0	0	0	0	0	0	0	12
<i>Maladera formosae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Neoserica</i> sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Nipponoserica</i> sp.1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Psilopholis gigantea</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Schoenherria hispida</i>	0	0	0	0	1	0	0	0	1	0	0	2	1	0	0	0	0	5
<i>Serica</i> sp.1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3
<i>Tetraserica vientianeensis</i>	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3

Rutelinae	Melolonthinae sp.1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2
	<i>Adoretus compressus</i>	0	0	3	0	4	0	0	6	13	0	1	4	0	0	0	0	31
	<i>Adoretus sinicus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
	<i>Adoretus</i> sp.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
	<i>Anomala concha</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Anomala matricula</i>	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
	<i>Anomala felicia</i>	0	0	0	2	0	1	0	0	7	0	0	0	0	0	0	0	10
	<i>Anomala pallida</i>	2	0	1	1	0	0	0	5	10	4	0	16	0	0	8	0	49
	<i>Anomala ptenomeloides</i>	0	0	0	0	0	0	0	16	4	0	0	3	1	5	0	1	30
	<i>Anomala sarawakensis</i>	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	4
	<i>Anomala</i> sp. 1	2	0	0	0	0	0	0	0	0	0	0	12	0	0	0	1	15
	<i>Anomala</i> sp. 2	2	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	7
	<i>Anomala</i> sp. 3	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	3
	<i>Anomala</i> sp. 4	0	0	0	0	0	1	0	0	0	0	0	17	0	0	0	0	18
	<i>Callistethus</i> sp.1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
	<i>Callistethus hamus</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	5
	<i>Mimela</i> sp.1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Mimela</i> sp.2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Mimela chrysoprasa</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Mimela maculicollis</i>	6	0	0	0	0	0	0	0	3	1	1	0	0	1	3	0	15

Scarabaeinae	<i>Parastasia</i> sp.1	0	0	0	0	1	1	0	0	3	0	0	0	0	1	0	0	1	7
	<i>Parastasia discolor</i>	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
	<i>Parastasia ephippium</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2
	Rutelinae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	2	0	18
	Rutelinae sp.2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	<i>Spinanomala</i> sp.1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	<i>Strigoderma</i> sp.1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Bolbochromus catenatus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	<i>Catharsius dayacus</i>	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	<i>Catharsius</i> sp. 1	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	4
	<i>Catharsius</i> sp. 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	<i>Copris</i> sp. 1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	2
	<i>Copris</i> sp. 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	<i>Gymnopleurus maurus</i>	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3
	<i>Ochicanthon</i> sp.1	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
	<i>Onthophagus aurifex</i>	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Onthophagus carinensis</i>	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
	<i>Onthophagus deliensis</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2
	<i>Onthophagus rudis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1

<i>Onthophagus sarawacus</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2	
<i>Onthophagus semiaureus</i>	74	2	0	0	0	1	0	0	2	0	0	39	0	2	0	0	0	120	
<i>Onthophagus semicupreus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Onthophagus vulpes</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	
<i>Onthophagus</i> sp. 1	1	0	0	0	0	0	0	0	2	1	0	7	1	1	0	1	0	14	
<i>Onthophagus</i> sp. 2	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	3	
<i>Onthophagus</i> sp. 3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	
<i>Onthophagus</i> sp. 4	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	5	
<i>Onthophagus</i> sp. 5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
<i>Onthophagus</i> sp. 6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
<i>Paragymnopleurus striatus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	
Scarabaeinae sp.1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	7	1	0	10	
Scarabaeinae sp.2	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	4	
Scarabaeinae sp.3	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	3	
Scarabaeinae sp.4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	3	
<i>Sisphus</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	
Total	126 species	302	64	80	14	21	46	50	139	214	53	25	311	58	26	102	21	25	1551

Appendix B

Subfamily	Species	Occurrence (/ - Occurred, 0 - Not occur)																	
		G	R	K	A	M	S	G	S	S	L	L	S	G	F	G	G	N	Total
		G	L	S	B	S	A	N	m	b	B	H	W	T	C	p	R	N	
		N	L	L	R				t	k	N	N	S					P	
		P									P	P							
Cetoniinae	<i>Agestrata orichalcea</i>	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Agestrata belitungana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	1
	<i>Chalcothea affinis</i>	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	1
	<i>Ixorida regia sumatrana</i>	0	0	0	0	0	/	0	0	/	/	0	0	/	0	/	0	/	6
	<i>Protaetia</i> sp.1	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Taeniodera inermis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	1
	<i>Taeniodera monacha</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	1
	<i>Taeniodera</i> sp.1	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
	Cetoiinae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	/	0	2
	Cetoiinae sp.2	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	1
	Cetoiinae sp.3	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	1
Aphodiinae	<i>Aphodius</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	1
	<i>Aphodius</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	1
Dynastinae	<i>Chalcosoma atlas</i>	/	0	0	0	/	/	/	/	0	/	0	/	/	/	0	0	0	9

	<i>Allomyrina pfeifferi pfeifferi</i>	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	1
	<i>Dichodontus coronatus</i>	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
	<i>Oryctes</i> sp.1	0	0	0	0	0	0	/	/	0	0	0	0	0	0	0	0	0	2
	<i>Oryctes gnu</i>	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
	<i>Oryctes rhinoceros</i>	0	/	/	0	0	0	0	/	/	0	0	0	0	0	/	0	/	6
	<i>Temnorhynchus baal</i>	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	1
	<i>Trichogomphus lunicollis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	1
	<i>Xylotrupes gideon</i>	0	0	0	0	0	0	0	/	/	0	/	0	0	0	0	0	0	3
	<i>Xylotrupes gideon borneensis</i>	0	0	0	0	0	/	/	0	0	0	0	0	0	/	/	0	/	5
Melolonthinae	<i>Apogonia</i> sp. 1	/	0	0	0	0	0	0	0	/	0	/	0	/	/	0	0	/	6
	<i>Apogonia</i> sp. 2	0	/	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	2
	<i>Apogonia</i> sp. 3	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	2
	<i>Apogonia</i> sp. 4	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Apogonia</i> sp. 5	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Apogonia</i> sp. 6	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Apogonia expeditionis</i>	0	/	/	/	/	/	/	/	/	/	/	/	0	0	0	0	0	11
	<i>Apogonia destructor</i>	0	0	/	0	/	/	/	/	/	/	/	/	/	/	/	/	0	13
	<i>Apogonia palawana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	1
	<i>Apogonia ritsemae</i>	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1

<i>Apogonia waterstradti</i>	0	0	/	0	0	/	/	/	/	/	/	/	0	/	/	0	0	10
<i>Adoretus compressus</i>	0	0	0	0	0	0	0	0	0	0	/	0	0	0	/	/	0	3
<i>Asactopholis pectoralis</i>	0	0	0	0	0	/	0	0	/	0	0	0	0	0	0	0	/	3
<i>Catharsius</i> sp.1	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Exopholis</i> sp.1	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Exopholis hypoleuca</i>	0	0	0	0	0	0	/	0	/	0	0	0	0	0	0	0	0	2
<i>Holotrichia</i> sp.1	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Holotrichia loochooana</i>	0	0	0	0	0	/	/	/	0	0	0	0	0	0	0	0	0	3
<i>Holotrichia serrata</i>	/	/	/	/	/	/	0	/	/	0	/	0	/	/	/	/	0	13
<i>Hoplia</i> sp. 1	/	0	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	2
<i>Hoplia</i> sp. 2	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Hoplia</i> sp. 3	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Hoplia</i> sp. 4	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Hoplia</i> sp. 5	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Hoplia aurata</i>	0	0	0	0	0	0	0	0	/	/	0	0	0	0	0	0	0	2
<i>Lepidiota</i> sp.1	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
<i>Lepidiota caesia</i>	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1
<i>Lepidiota mellyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	1
<i>Lepidiota stigma</i>	0	0	0	0	0	0	0	/	0	0	0	0	0	0	/	0	0	2

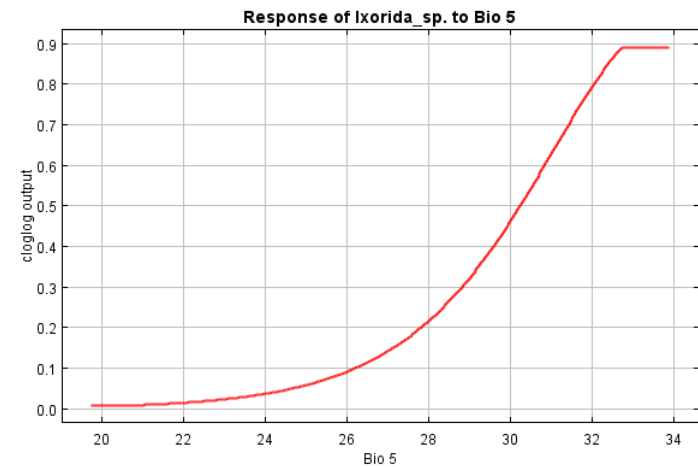
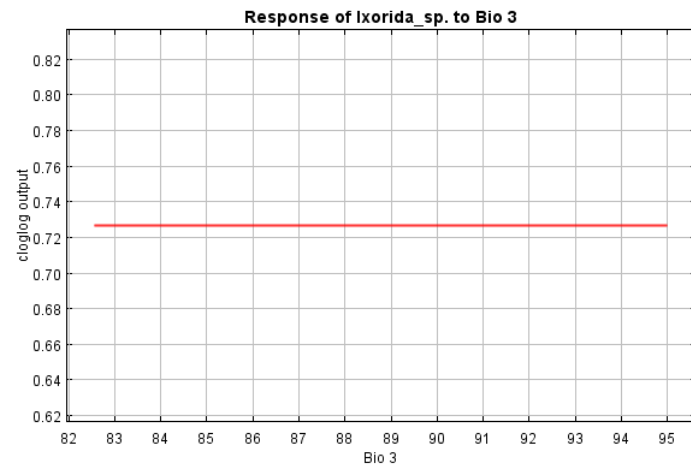
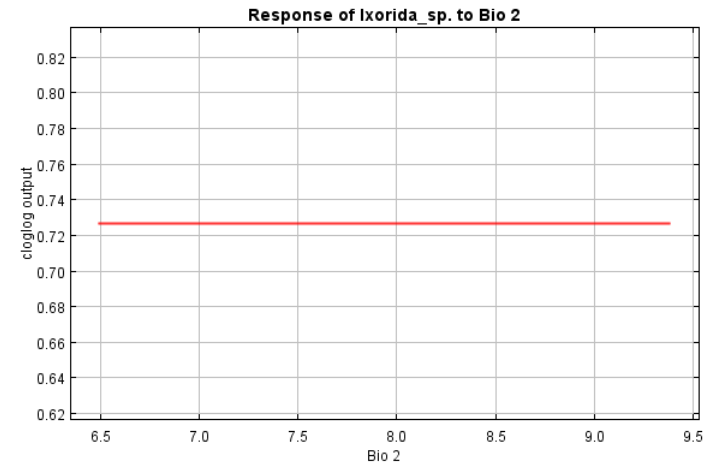
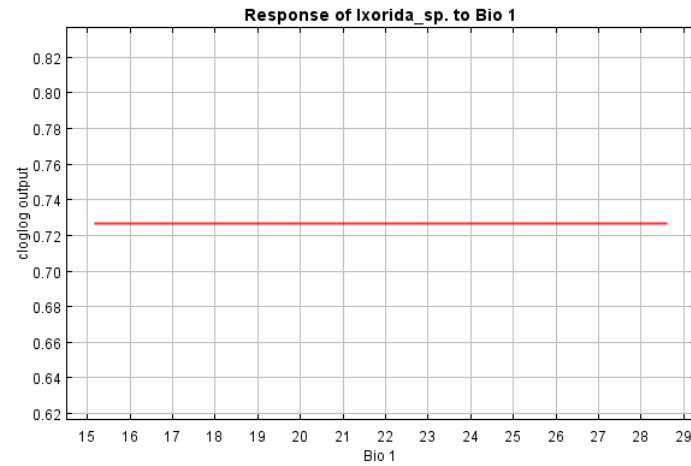
<i>Leucopholis emarginata</i>	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1
<i>Leucopholis staudingeri</i>	/	0	0	/	0	0	/	/	/	0	0	/	/	0	0	0	0	7
<i>Maladera</i> sp. 1	/	0	0	0	0	0	0	0	/	/	/	/	/	/	/	/	0	9
<i>Maladera</i> sp. 2	/	0	0	0	0	0	0	0	/	0	0	/	0	0	0	0	0	3
<i>Maladera</i> sp. 3	0	0	/	0	/	0	0	0	/	0	0	/	0	0	0	0	0	4
<i>Maladera</i> sp. 4	0	0	/	0	/	0	0	0	/	0	0	0	0	0	0	0	0	3
<i>Maladera</i> sp. 5	0	0	0	0	0	/	0	0	/	0	0	0	0	0	0	0	0	2
<i>Maladera</i> sp. 6	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Maladera</i> sp. 7	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Maladera</i> sp. 8	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Maladera</i> sp. 9	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Maladera castanea</i>	0	0	0	0	0	/	0	0	0	/	0	0	0	0	0	0	0	2
<i>Maladera formosae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	/	1
<i>Neoserica</i> sp.1	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1
<i>Nipponoserica</i> sp.1	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1
<i>Psilopholis gigantea</i>	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
<i>Schoenherria hispida</i>	0	0	0	0	/	0	0	0	/	0	0	/	/	0	0	0	0	4
<i>Serica</i> sp.1	0	0	/	/	0	/	0	0	0	0	0	0	0	0	0	0	0	3
<i>Tetraserica vientianeensis</i>	0	0	/	0	0	0	0	0	/	0	0	0	0	0	0	0	0	2

Rutelinae	Melolonthinae sp.1	0	0	0	0	0	0	0	0	0	/	0	/	0	0	0	0	0	2
	<i>Adoretus compressus</i>	0	0	/	0	/	0	0	/	/	0	/	/	0	0	0	0	0	6
	<i>Adoretus sinicus</i>	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	1
	<i>Adoretus</i> sp.1	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
	<i>Anomala concha</i>	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Anomala matricula</i>	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Anomala felicia</i>	0	0	0	/	0	/	0	0	/	0	0	0	0	0	0	0	0	3
	<i>Anomala pallida</i>	/	0	/	/	0	0	0	/	/	/	0	/	0	0	/	0	/	9
	<i>Anomala ptenomeloides</i>	0	0	0	0	0	0	0	/	/	0	0	/	/	/	0	/	0	6
	<i>Anomala sarawakensis</i>	0	0	0	0	0	0	0	/	/	0	0	0	0	0	0	0	0	2
	<i>Anomala</i> sp. 1	/	0	0	0	0	0	0	0	0	0	0	/	0	0	0	/	0	3
	<i>Anomala</i> sp. 2	/	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	2
	<i>Anomala</i> sp. 3	0	0	/	0	0	0	0	0	0	0	0	/	0	0	0	0	0	2
	<i>Anomala</i> sp. 4	0	0	0	0	0	/	0	0	0	0	0	/	0	0	0	0	0	2
	<i>Callistethus</i> sp.1	0	0	0	0	0	0	0	/	/	0	0	0	0	0	0	0	0	2
	<i>Callistethus hamus</i>	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	/	2
	<i>Mimela</i> sp.1	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Mimela</i> sp.2	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Mimela chrysoprasa</i>	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Mimela maculicollis</i>	/	0	0	0	0	0	0	0	/	/	/	0	0	/	/	0	0	6

Scarabaeinae	<i>Parastasia</i> sp.1	0	0	0	0	/	/	0	0	/	0	0	0	0	/	0	0	/	5
	<i>Parastasia discolor</i>	0	0	0	0	0	/	0	/	0	0	0	0	0	0	0	0	0	2
	<i>Parastasia ephippium</i>	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	/	2
	Rutelinae sp.1	0	0	0	0	0	0	0	0	0	0	0	0	/	0	0	/	0	2
	Rutelinae sp.2	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
	<i>Spinanomala</i> sp.1	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
	<i>Strigoderma</i> sp.1	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Bolbochromus catenatus</i>	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
	<i>Catharsius dayacus</i>	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Catharsius</i> sp. 1	0	0	0	0	0	0	0	0	/	/	/	0	0	0	0	0	0	3
	<i>Catharsius</i> sp. 2	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
	<i>Copris</i> sp. 1	0	0	0	0	0	/	0	0	0	/	0	0	0	0	0	0	0	2
	<i>Copris</i> sp. 2	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
	<i>Gymnopleurus maurus</i>	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	1
	<i>Ochicanthon</i> sp.1	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Onthophagus aurifex</i>	0	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Onthophagus carinensis</i>	/	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Onthophagus deliensis</i>	0	0	0	0	0	0	0	0	0	/	/	0	0	0	0	0	0	2
	<i>Onthophagus rudis</i>	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1

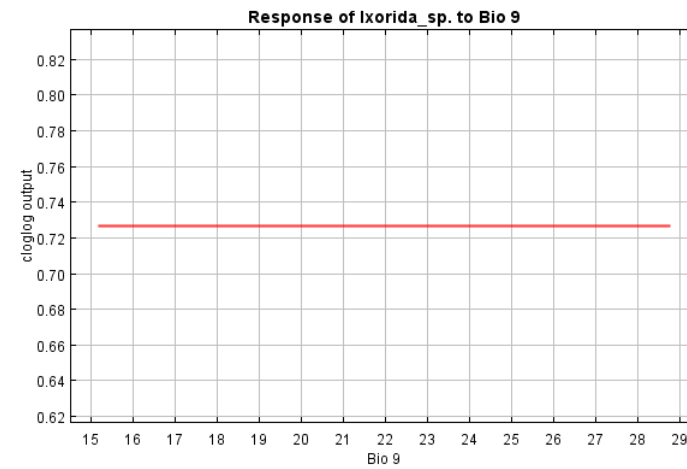
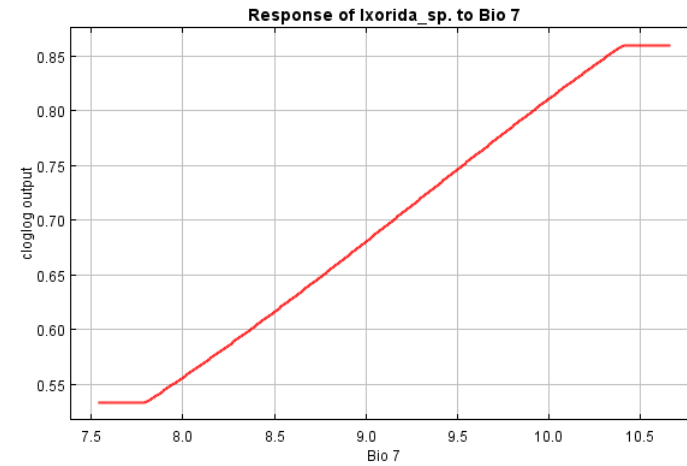
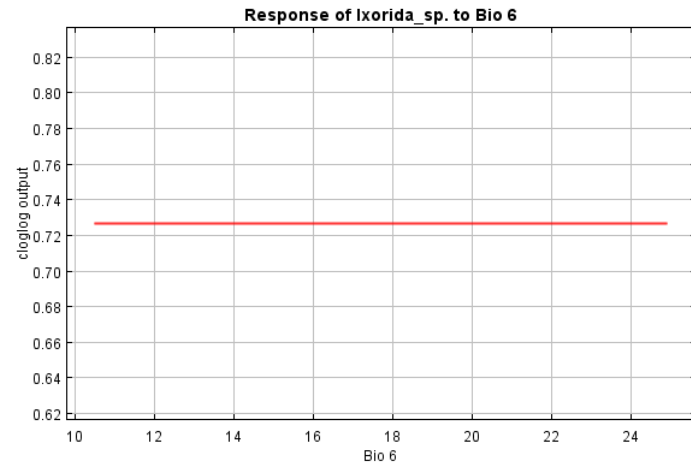
<i>Onthophagus sarawacus</i>	0	0	0	0	0	/	0	0	/	0	0	0	0	0	0	0	0	2
<i>Onthophagus semiaureus</i>	/	/	0	0	0	/	0	0	/	0	0	/	0	/	0	0	0	6
<i>Onthophagus semicupreus</i>	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	0	0	1
<i>Onthophagus vulpes</i>	0	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	1
<i>Onthophagus</i> sp. 1	/	0	0	0	0	0	0	0	/	/	0	/	/	/	0	/	0	7
<i>Onthophagus</i> sp. 2	0	0	0	0	0	/	0	0	0	0	0	0	/	0	0	/	0	3
<i>Onthophagus</i> sp. 3	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Onthophagus</i> sp. 4	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Onthophagus</i> sp. 5	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Onthophagus</i> sp. 6	0	0	0	0	0	0	0	/	0	0	0	0	0	0	0	0	0	1
<i>Paragymnopleurus striatus</i>	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	1
Scarabaeinae sp.1	0	0	0	0	0	0	0	0	/	0	0	0	0	/	/	/	0	4
Scarabaeinae sp.2	0	0	0	0	0	0	0	0	/	0	0	0	0	/	0	/	0	3
Scarabaeinae sp.3	0	0	0	0	0	0	0	0	/	0	0	0	0	/	0	/	0	3
Scarabaeinae sp.4	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	/	0	2
<i>Sisphus</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	/	0	0	0	0	0	1

Appendix C



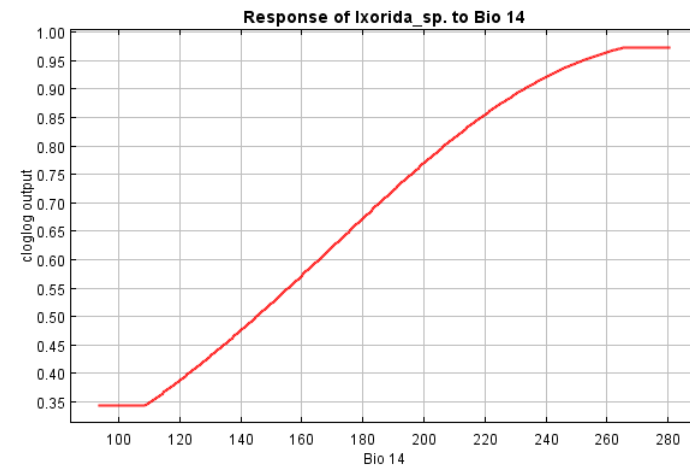
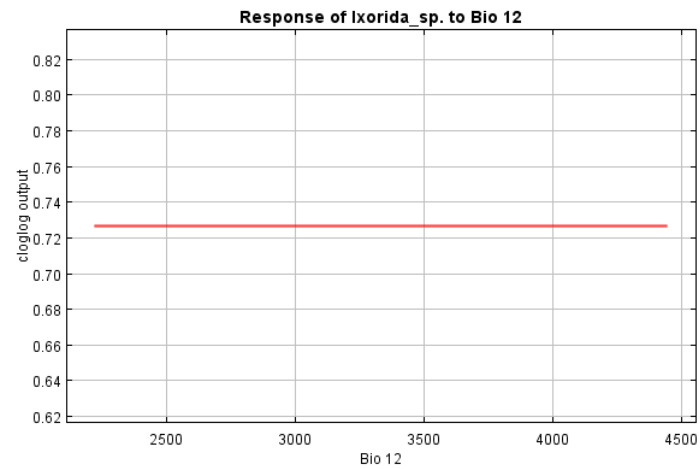
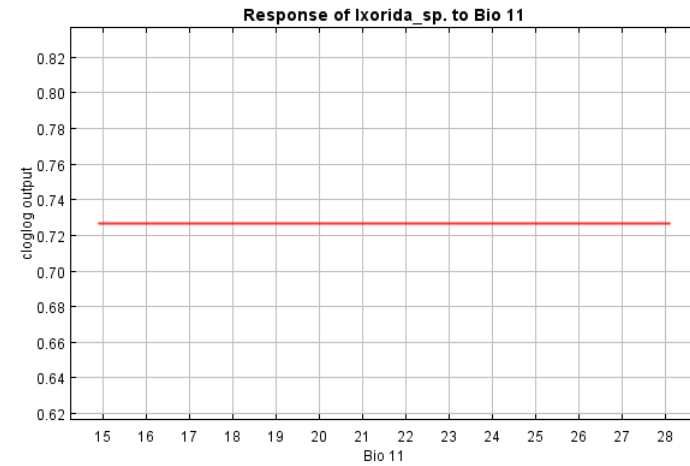
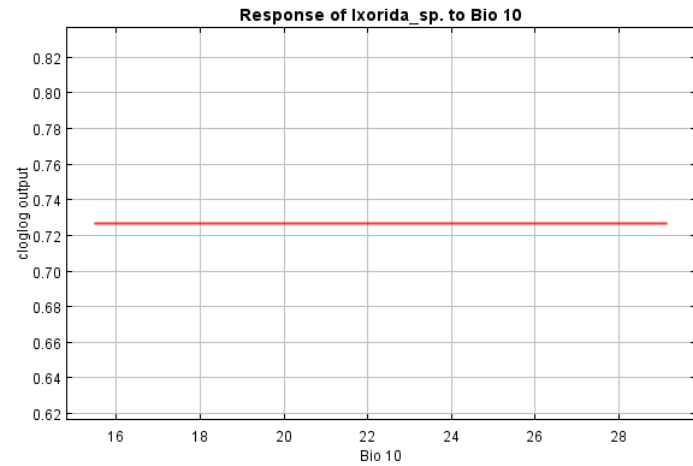
Response curves of MaxEnt model for *Ixorida* spp.

Appendix C continued



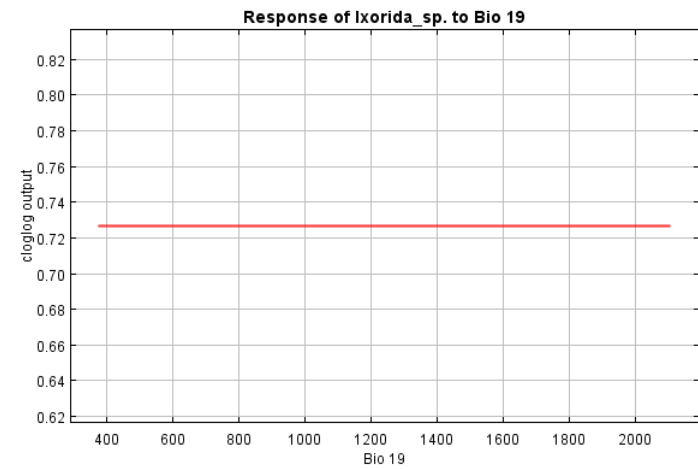
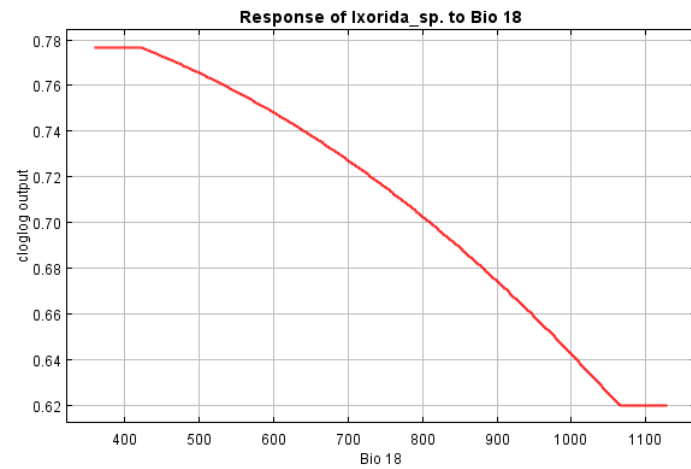
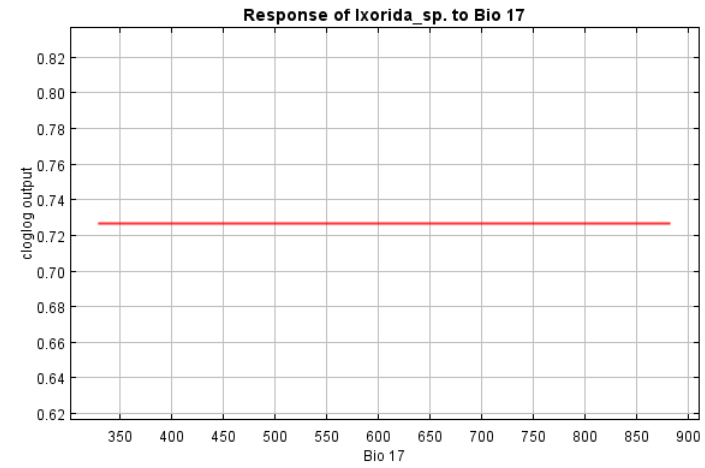
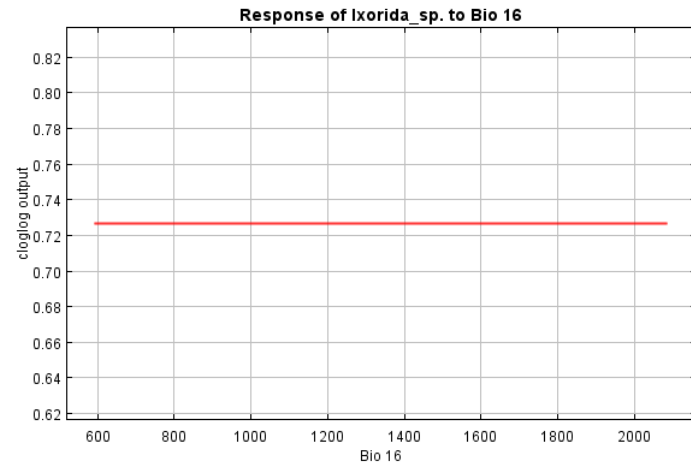
Response curves of MaxEnt model for *Ixorida* spp.

Appendix C continued



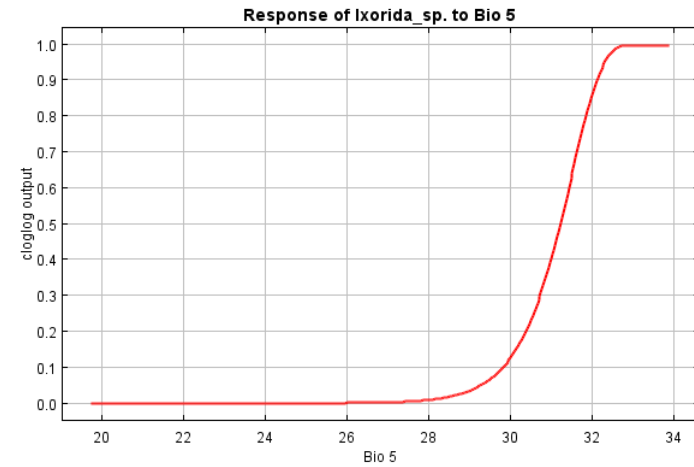
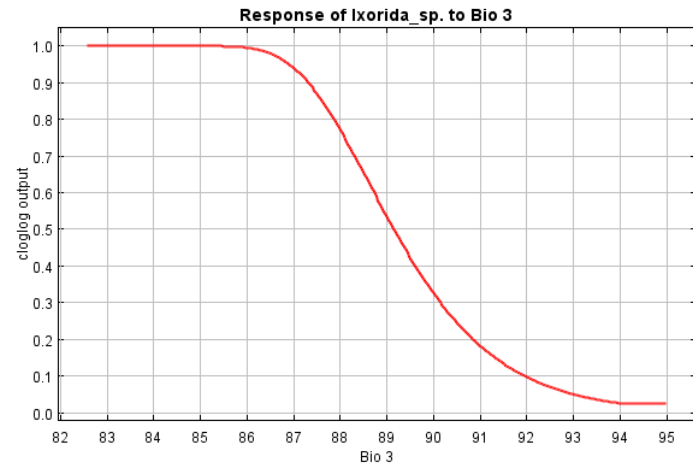
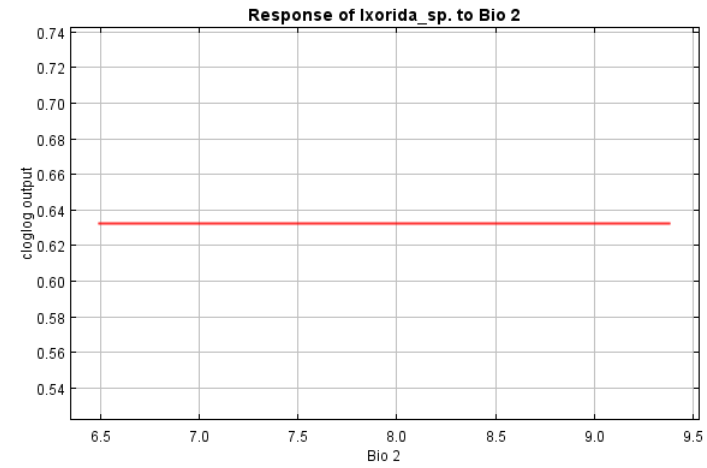
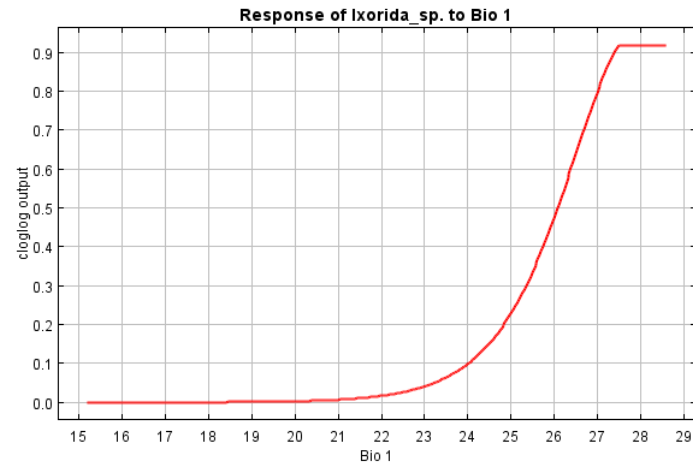
Response curves of MaxEnt model for *Ixorida* spp.

Appendix C continued



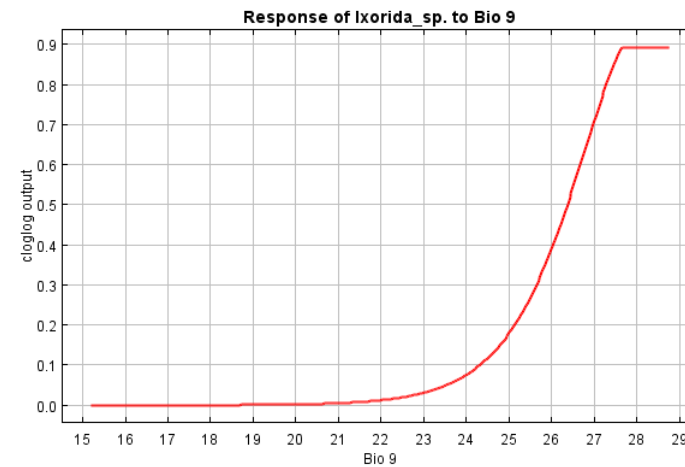
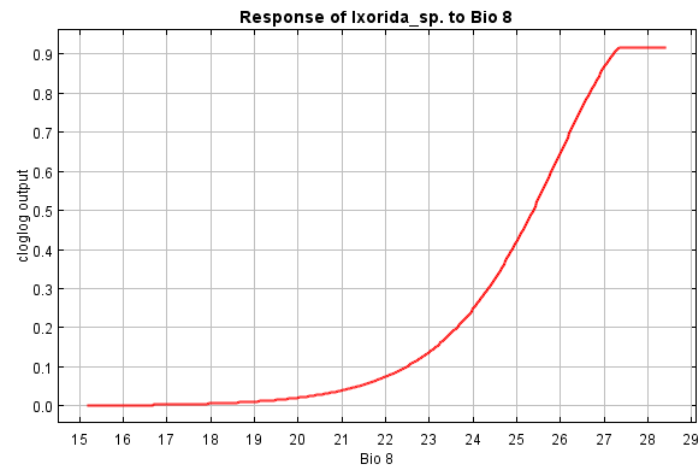
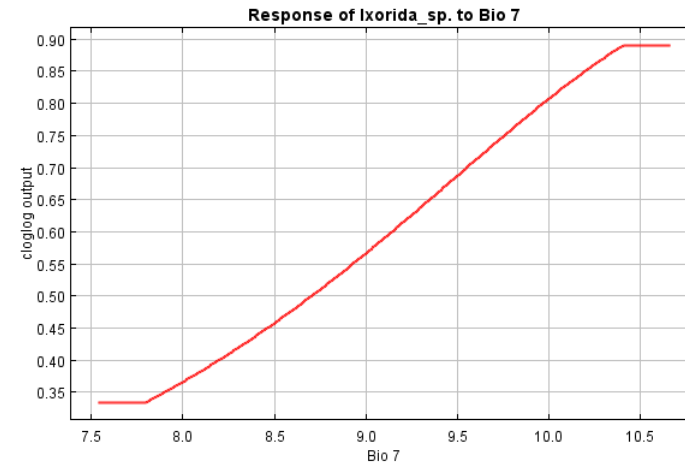
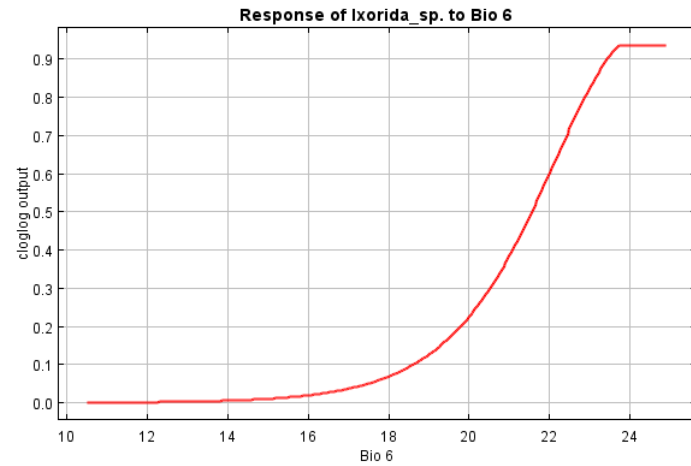
Response curves of MaxEnt model for *Ixorida* spp.

Appendix D



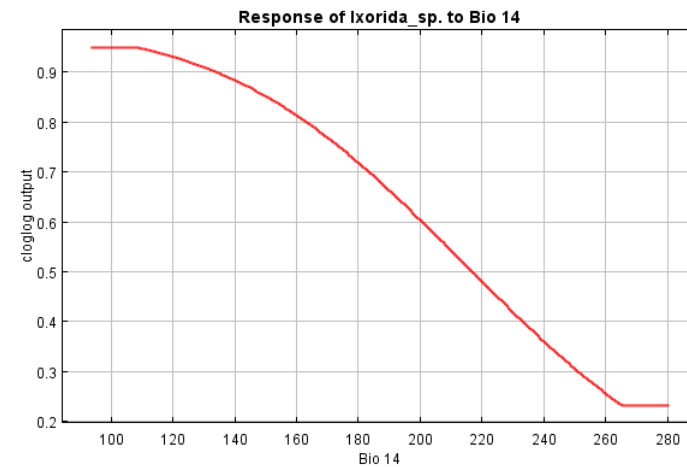
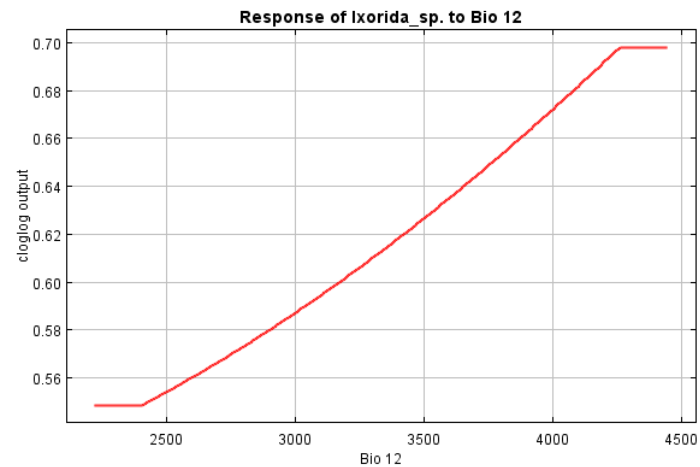
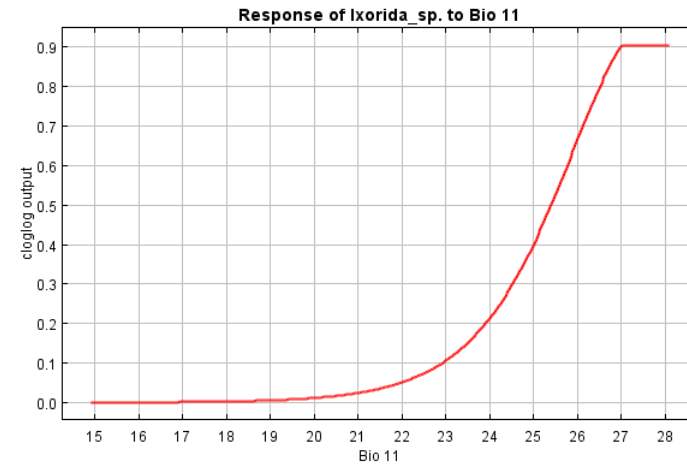
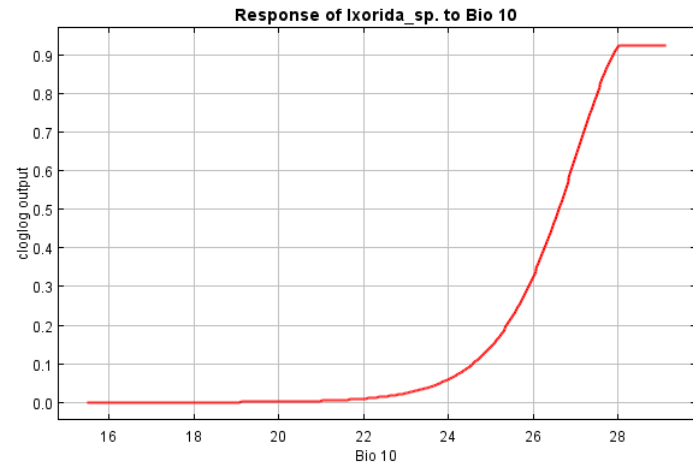
Response curves of MaxEnt model for *Ixorida* spp. using only corresponding variables.

Appendix D continued



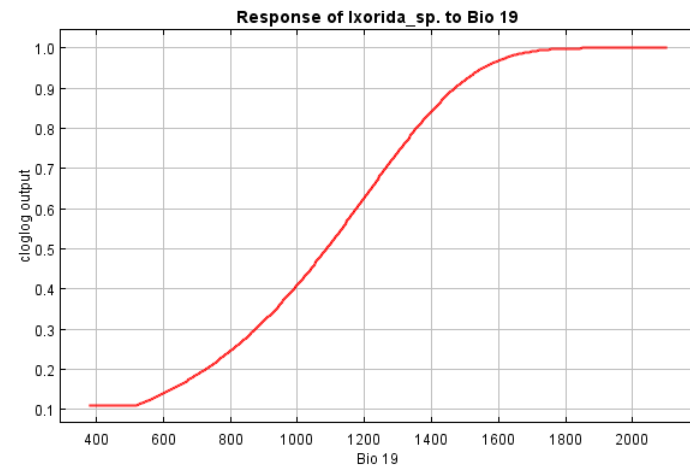
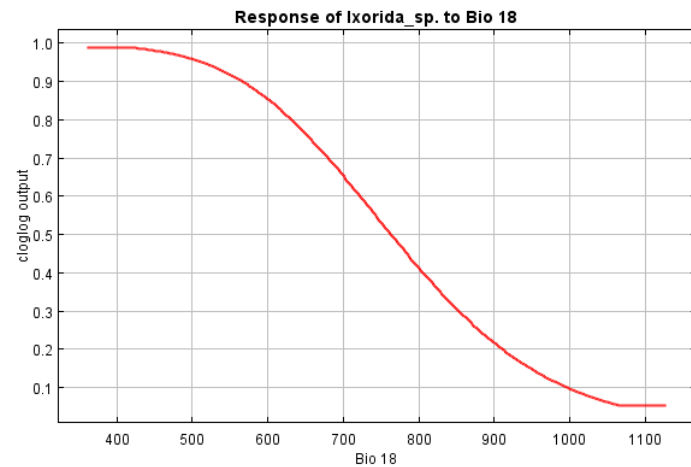
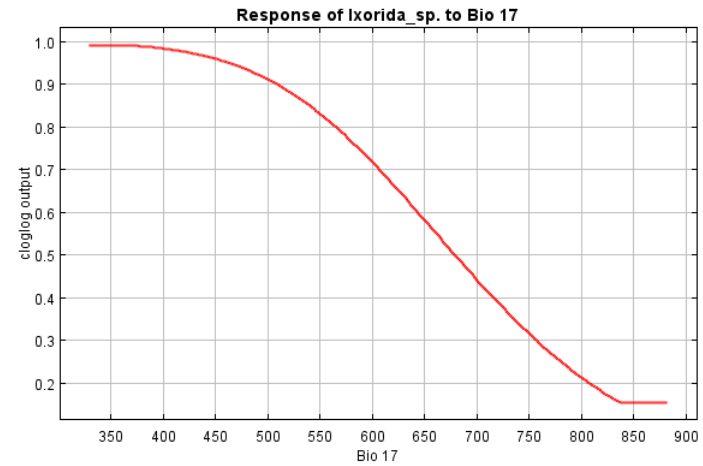
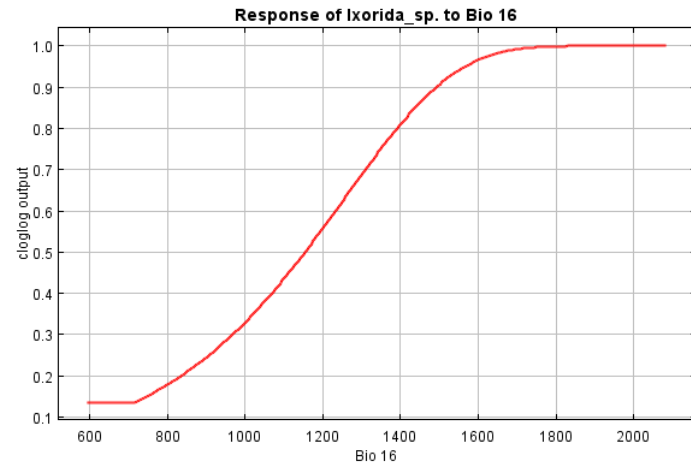
Response curves of MaxEnt model for *Ixorida* spp. using only corresponding variables.

Appendix D continued



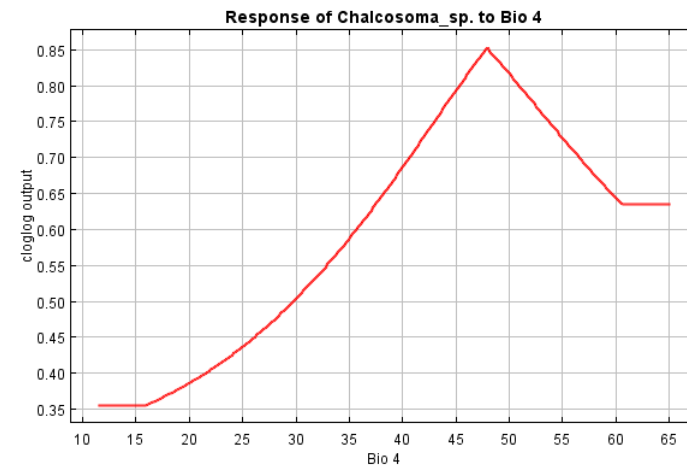
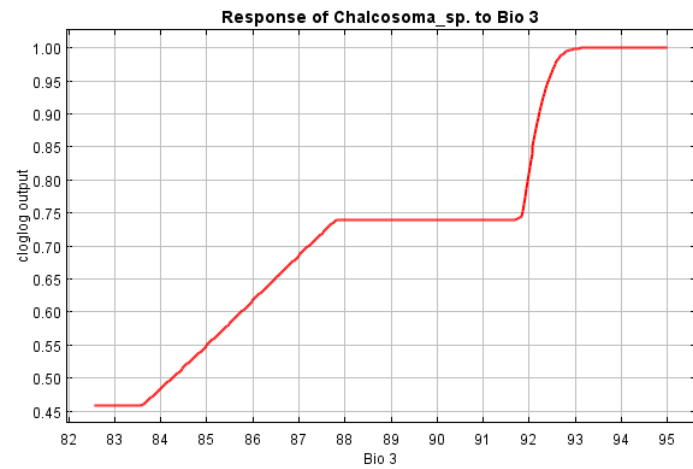
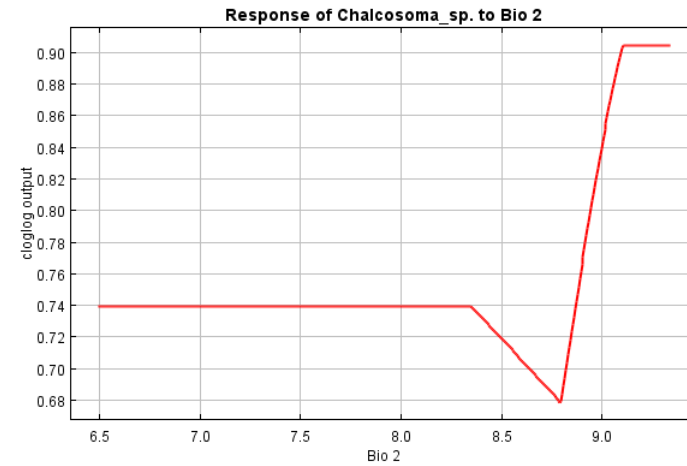
Response curves of MaxEnt model for *Ixorida* spp. using only corresponding variables.

Appendix D continued



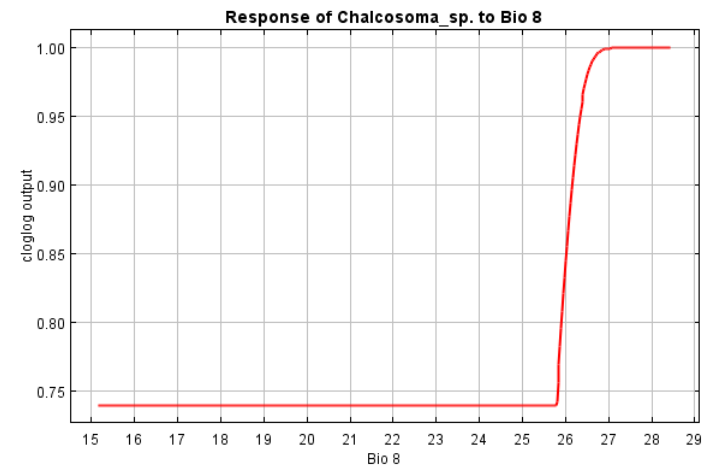
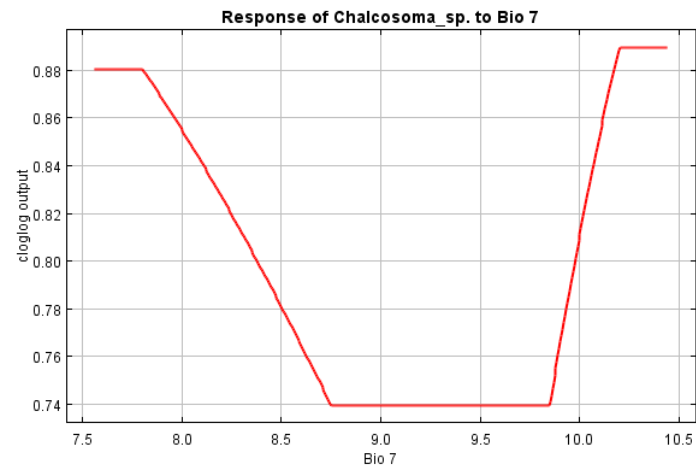
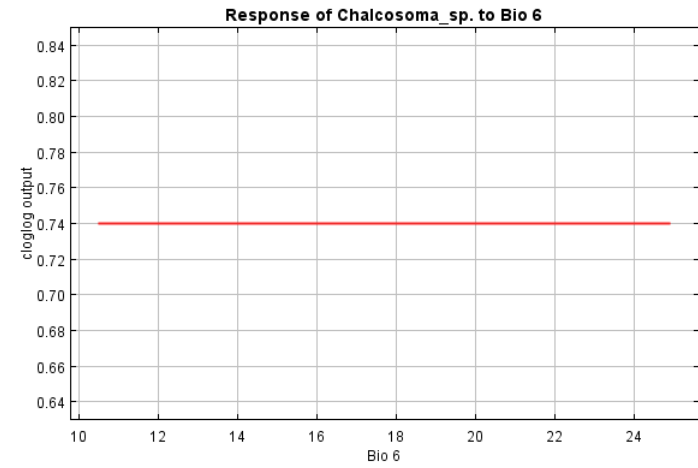
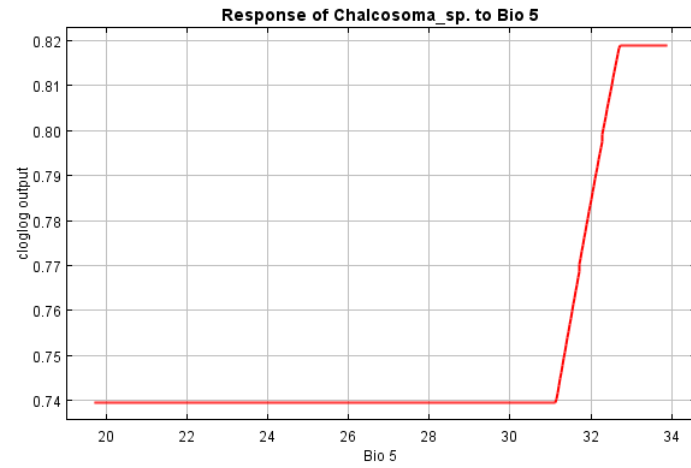
Response curves of MaxEnt model for *Ixorida* spp. using only corresponding variables.

Appendix E



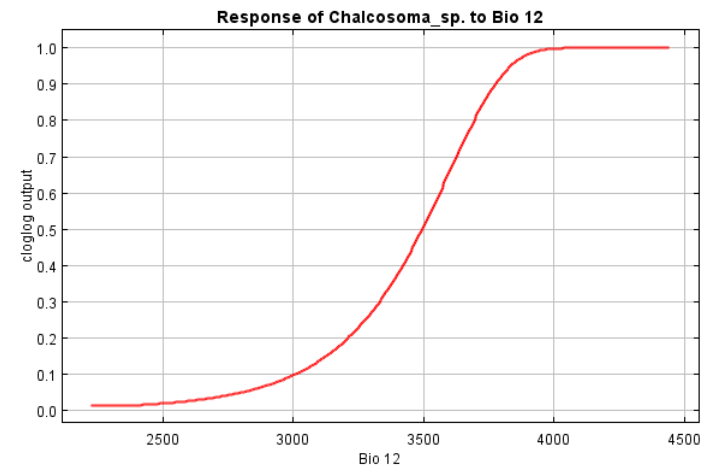
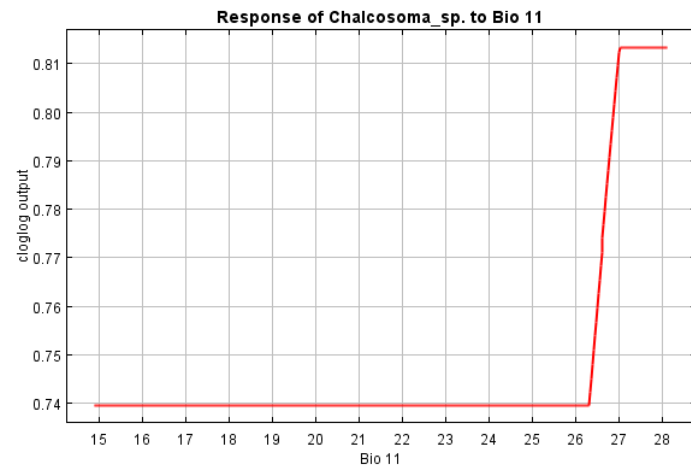
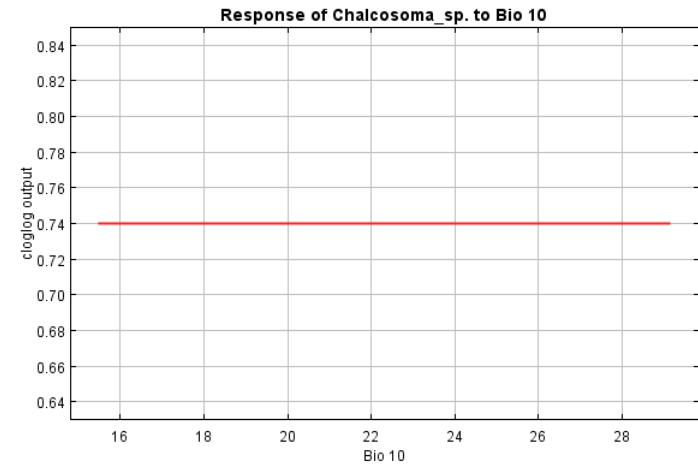
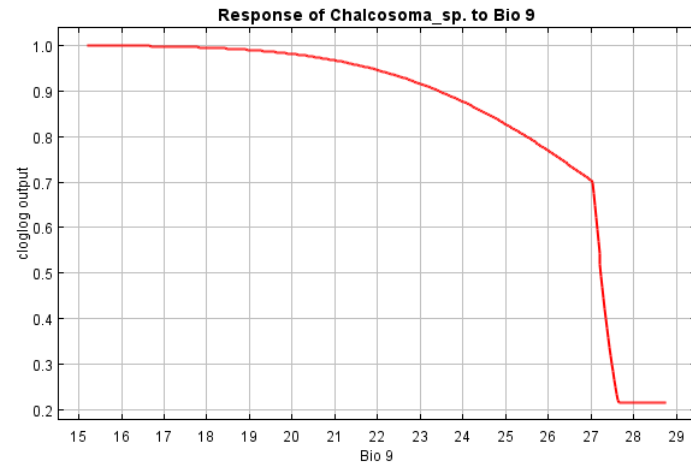
Response curves of MaxEnt model for *Chalcosoma* spp.

Appendix E continued



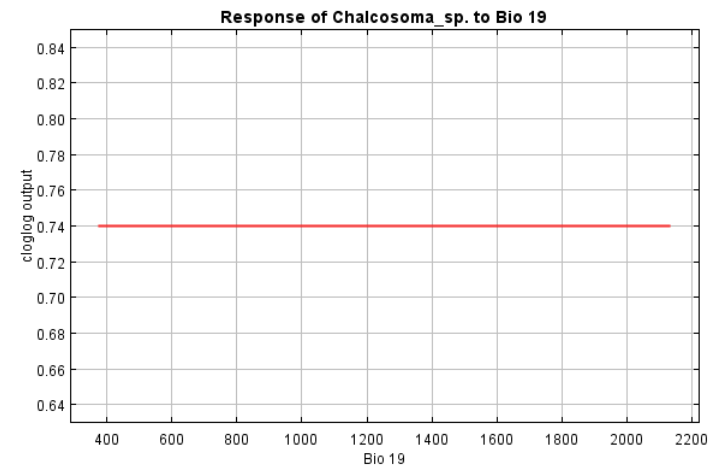
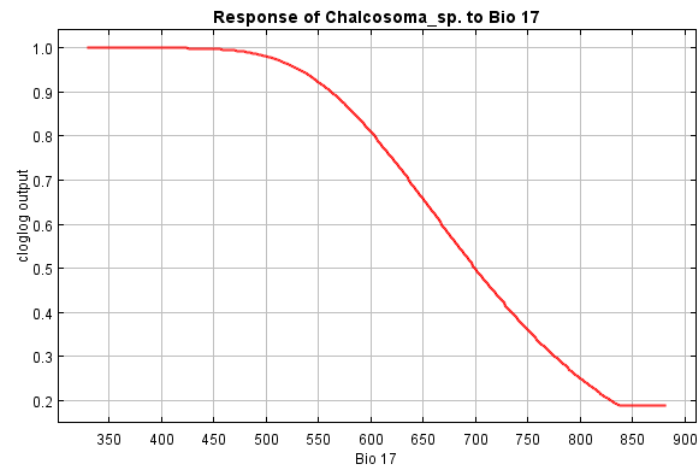
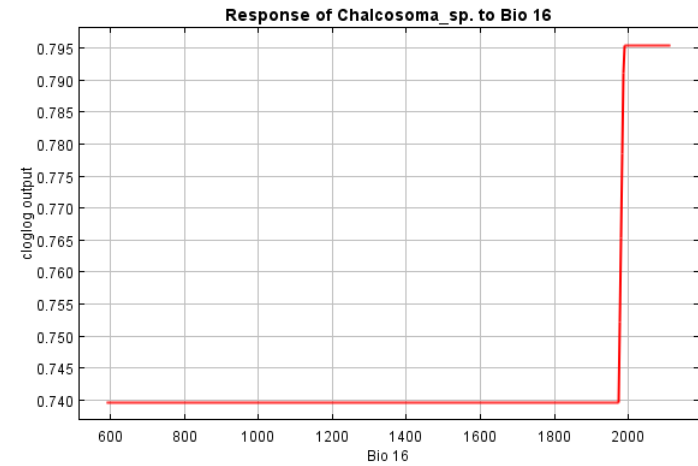
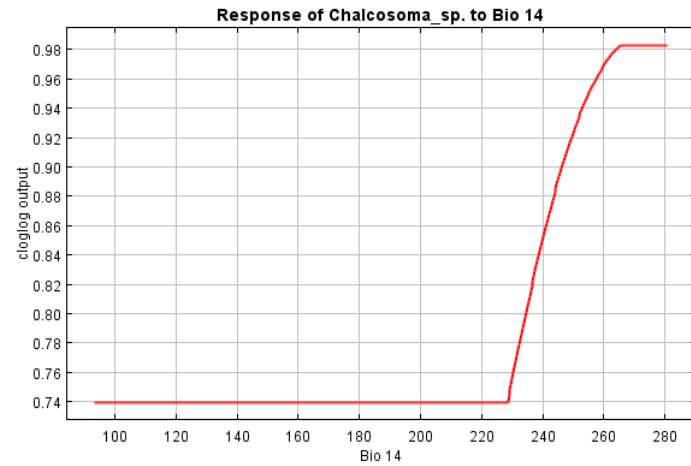
Response curves of MaxEnt model for *Chalcosoma* spp.

Appendix E continued



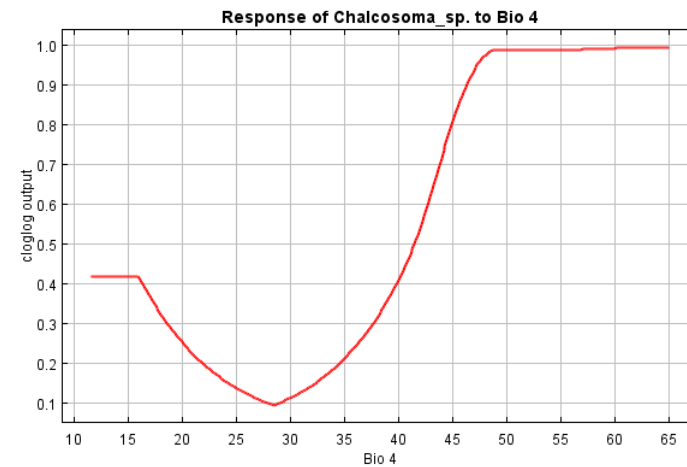
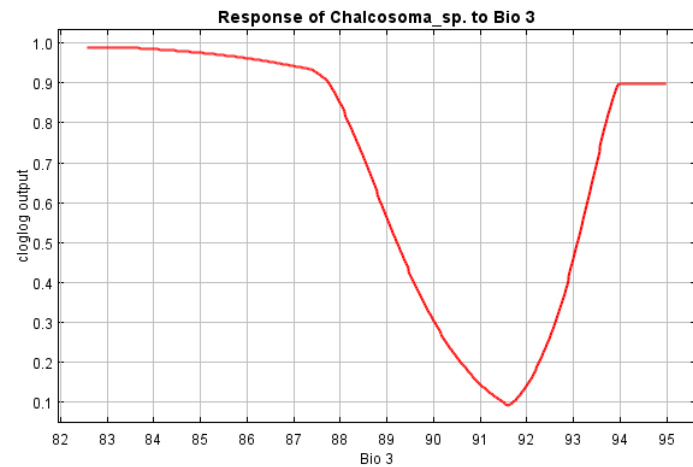
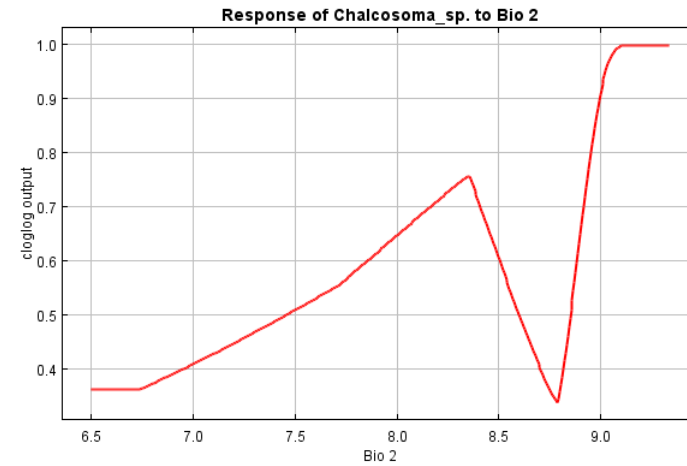
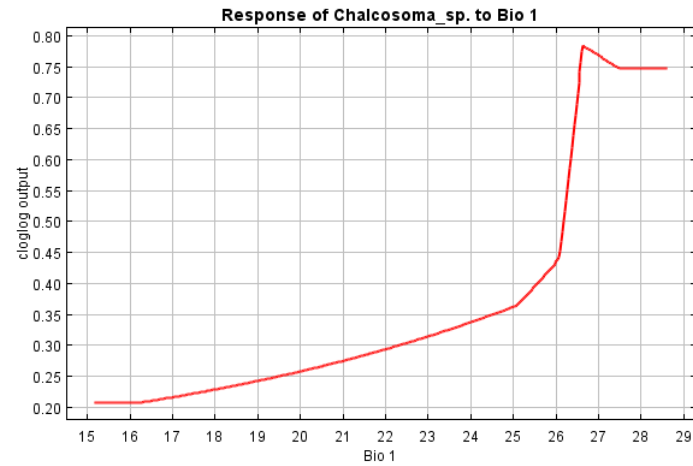
Response curves of MaxEnt model for *Chalcosoma* spp.

Appendix E continued



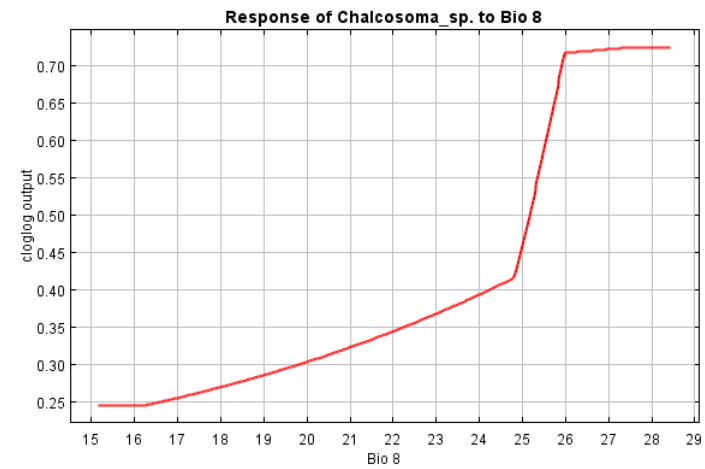
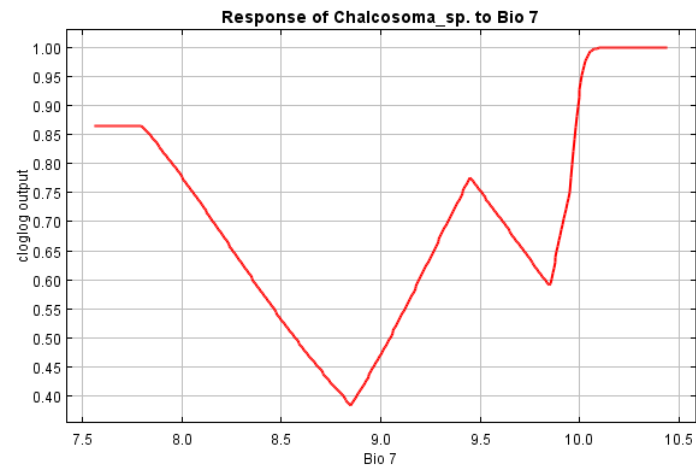
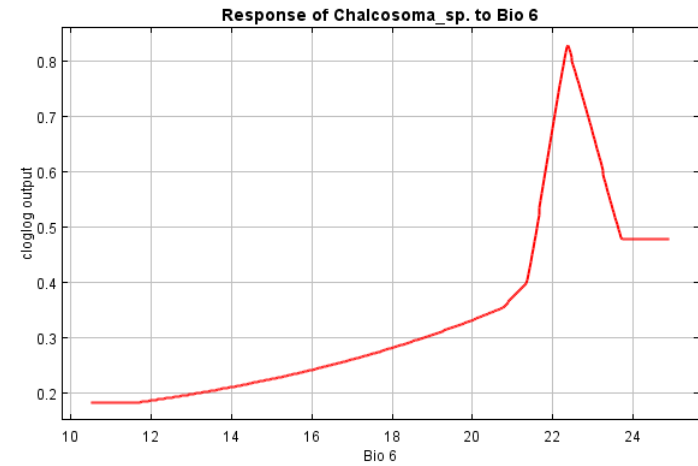
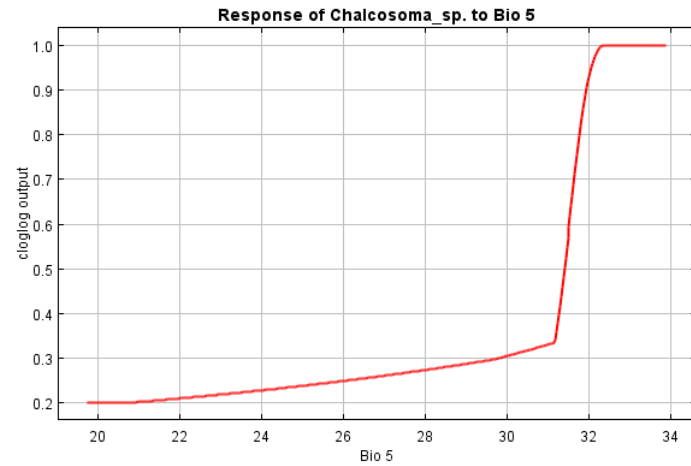
Response curves of MaxEnt model for *Chalcosoma* spp.

Appendix F



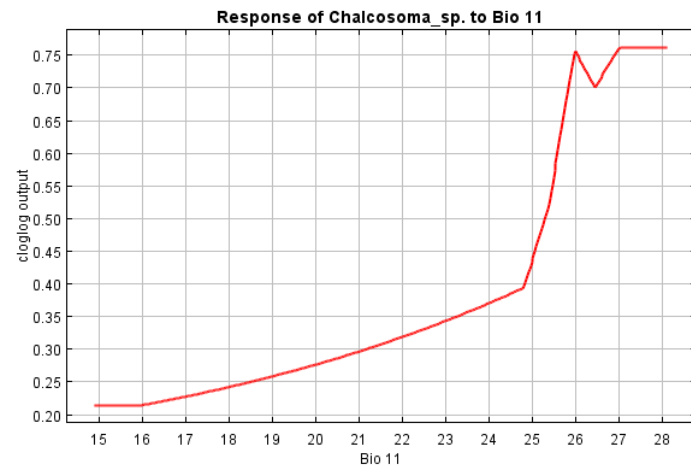
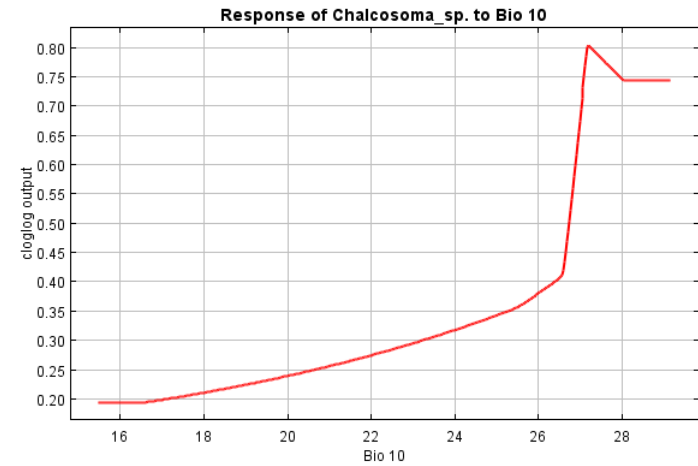
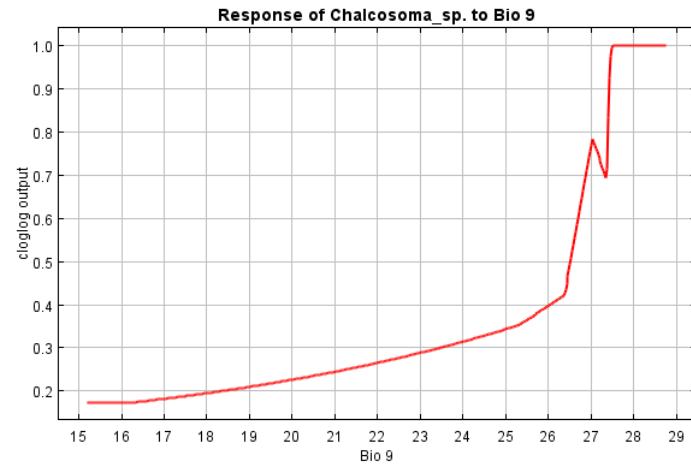
Response curves of MaxEnt model for *Chalcosoma* spp. using only corresponding variables.

Appendix F continued



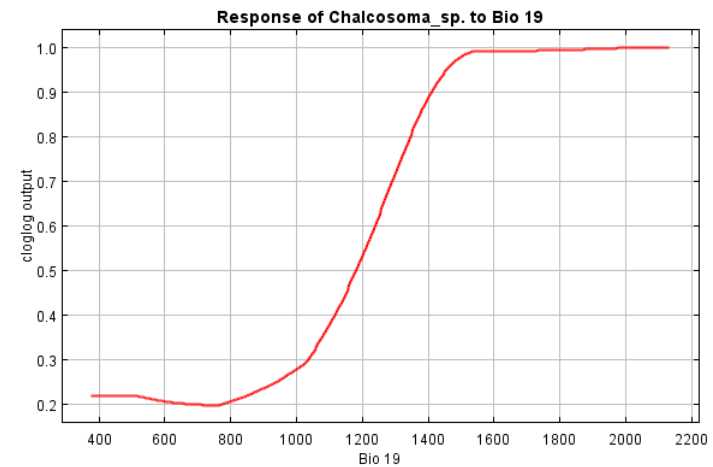
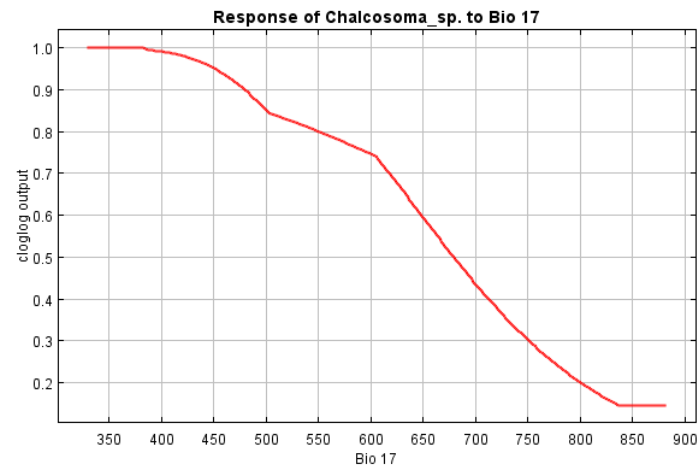
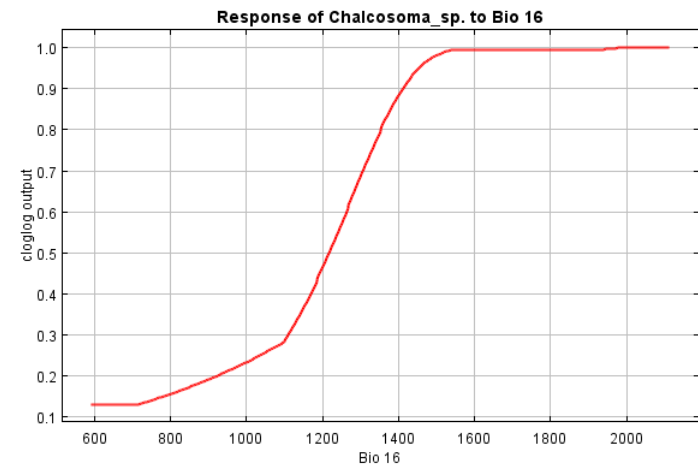
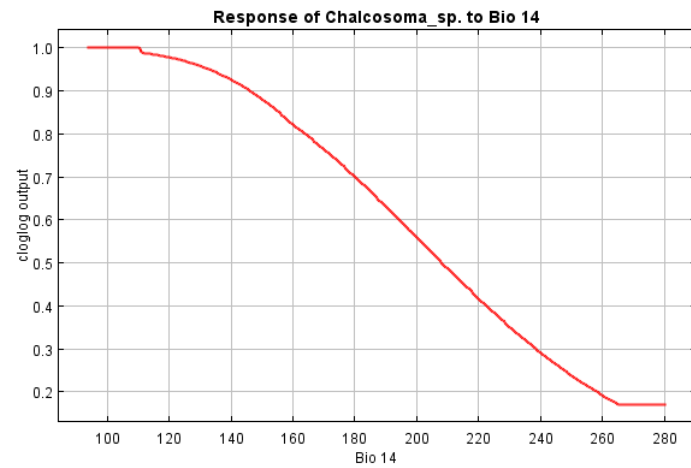
Response curves of MaxEnt model for *Chalcosoma* spp. using only corresponding variables.

Appendix F continued



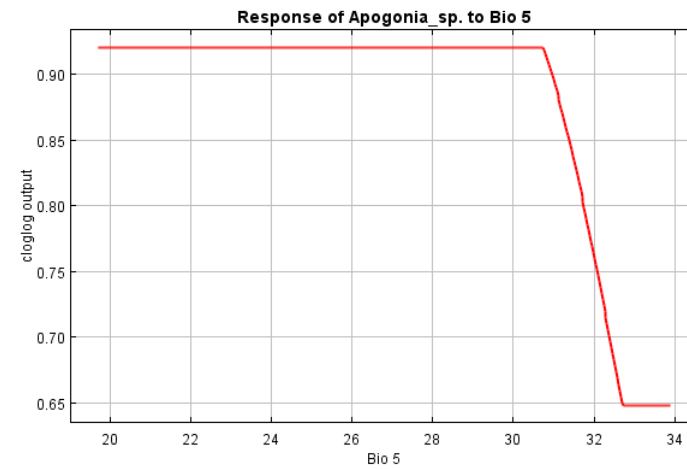
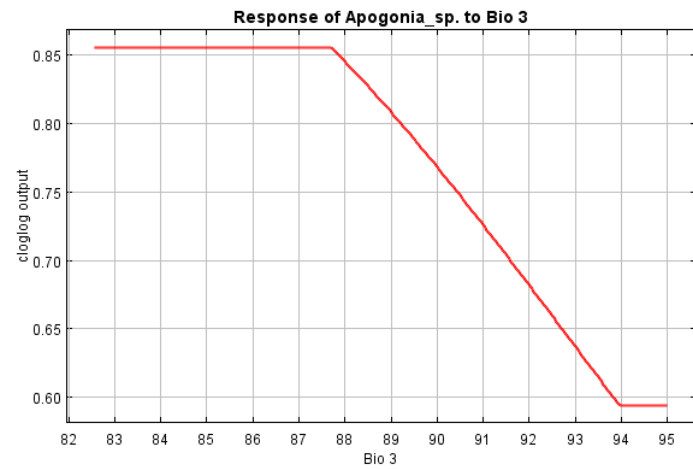
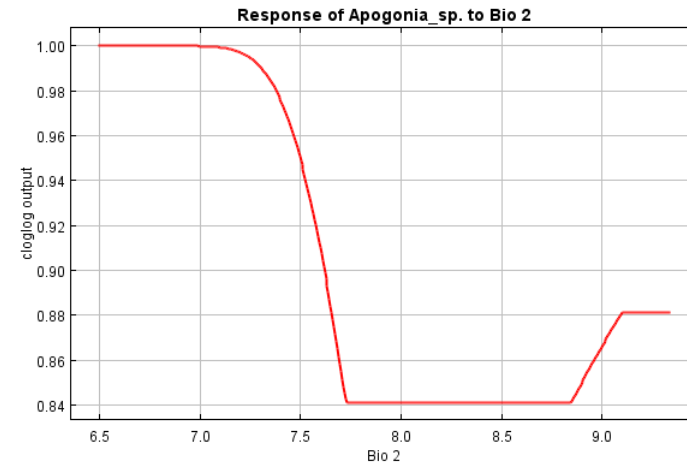
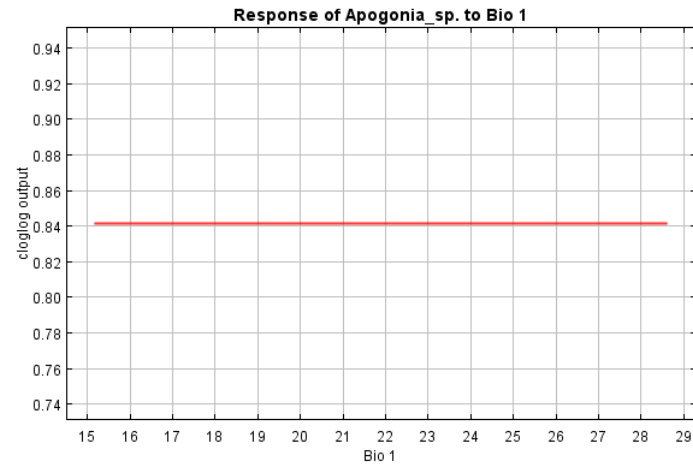
Response curves of MaxEnt model for *Chalcosoma* spp. using only corresponding variables.

Appendix F continued



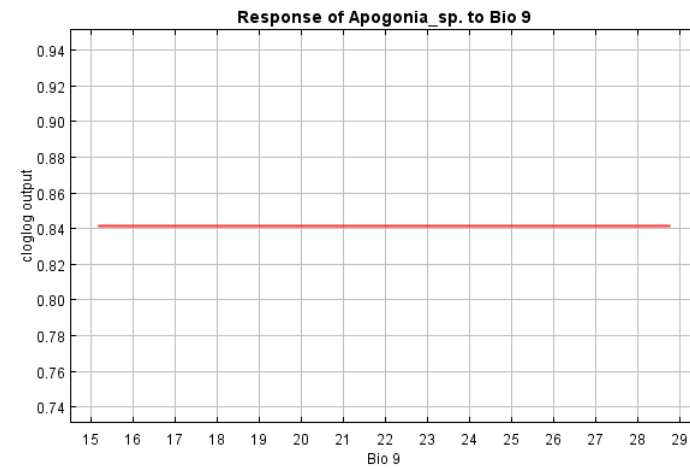
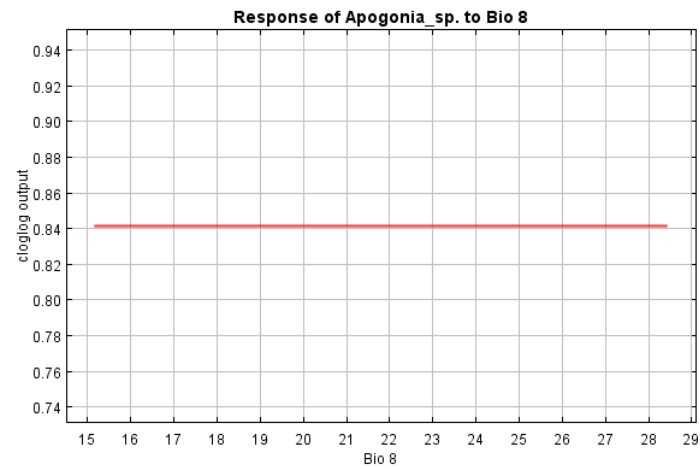
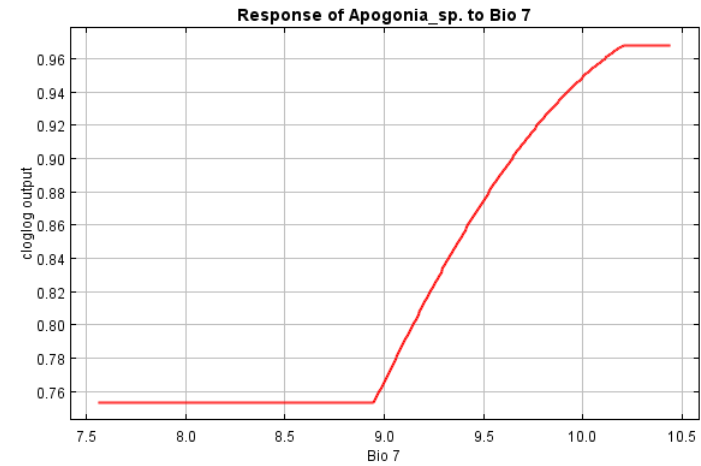
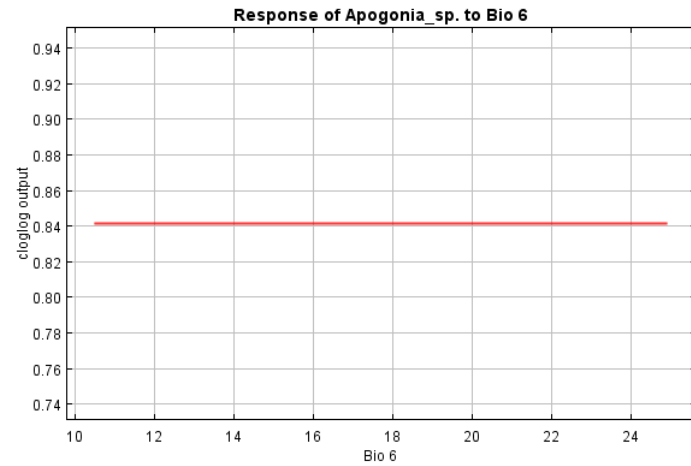
Response curves of MaxEnt model for *Chalcosoma* spp. using only corresponding variables.

Appendix G



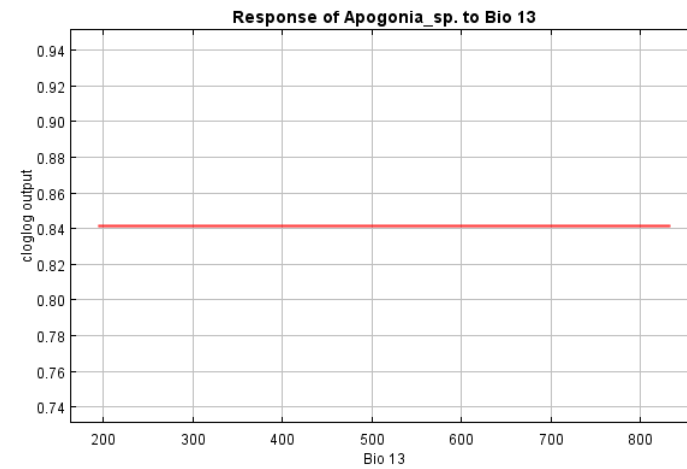
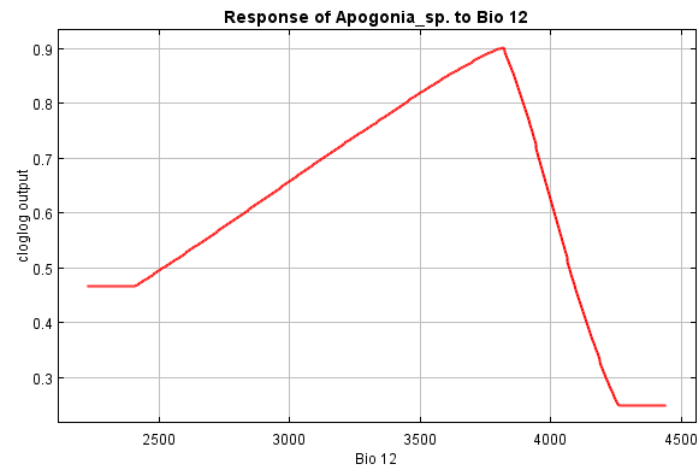
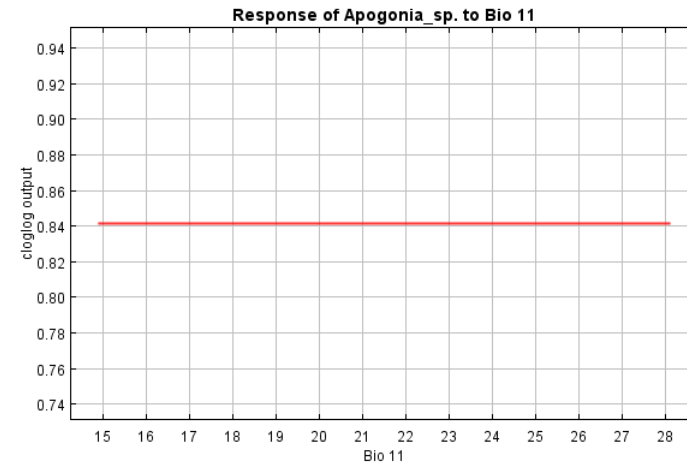
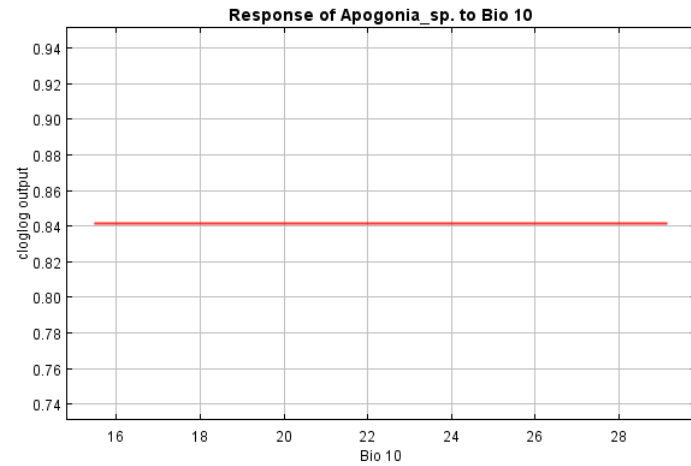
Response curves of MaxEnt model for *Apogonia* spp.

Appendix G continued



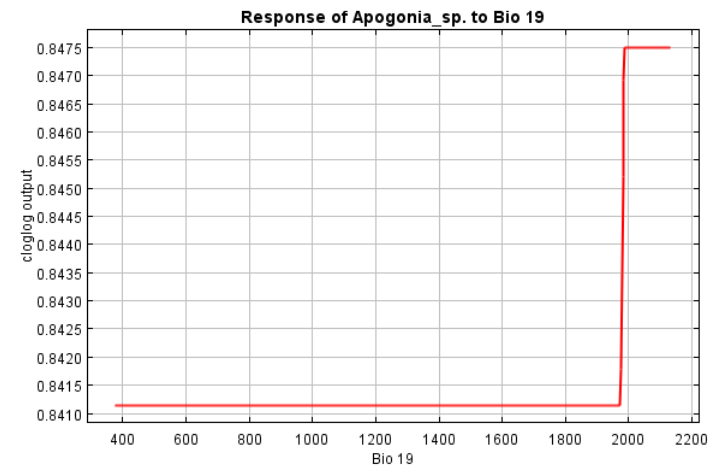
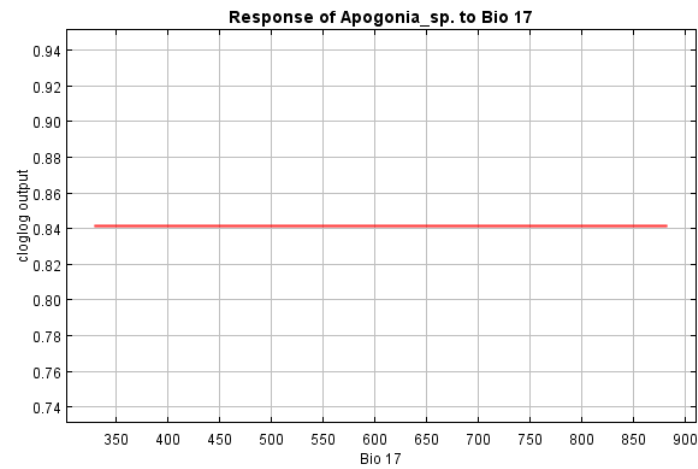
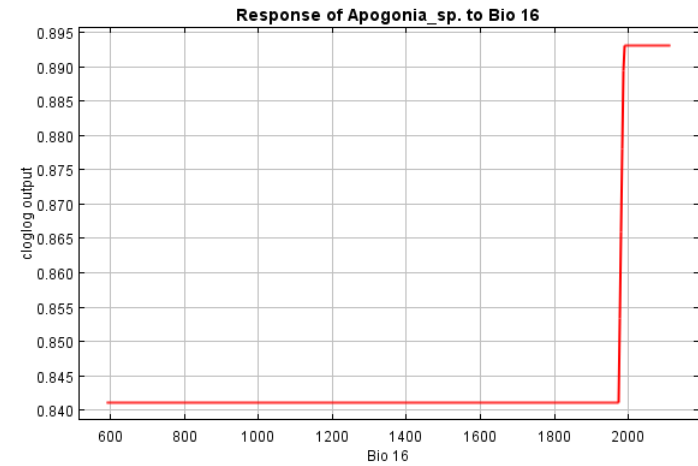
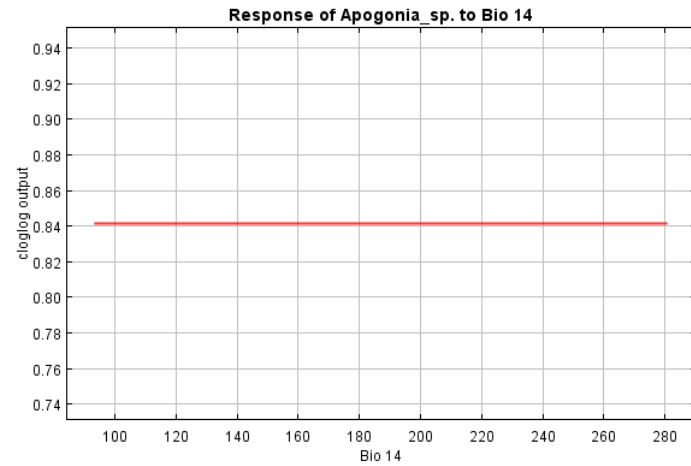
Response curves of MaxEnt model for *Apogonia* spp.

Appendix G continued



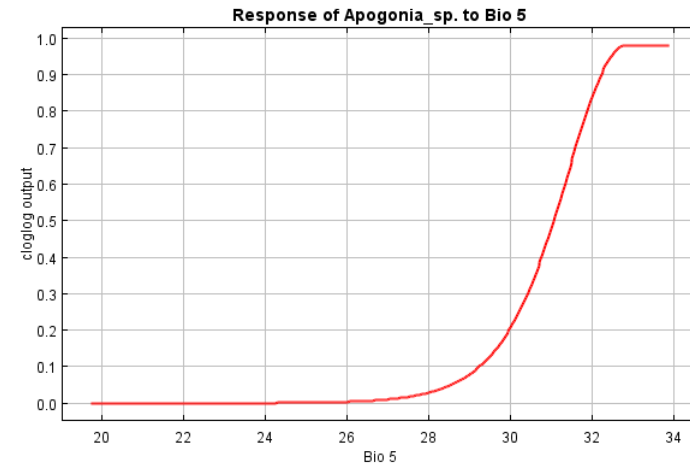
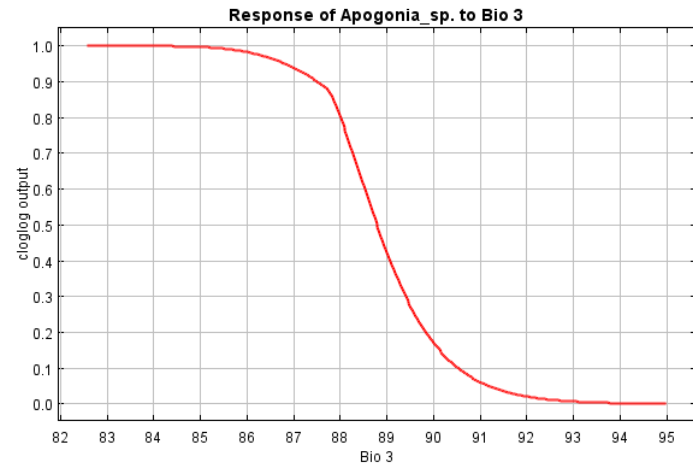
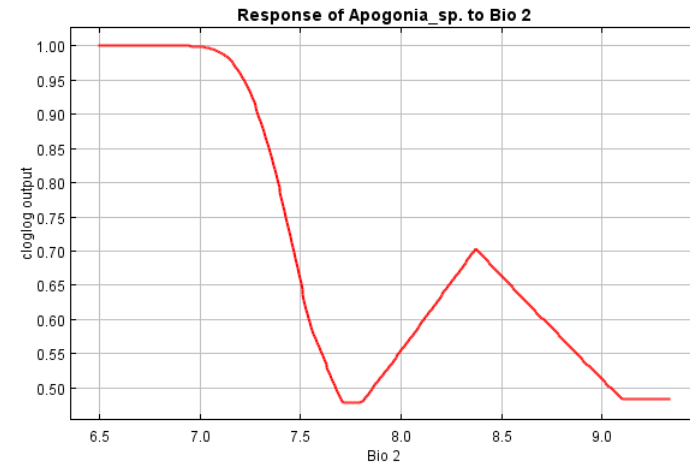
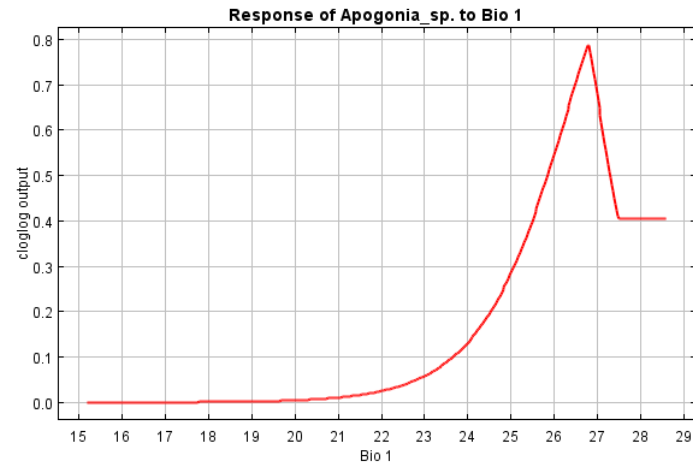
Response curves of MaxEnt model for *Apogonia* spp.

Appendix G continued



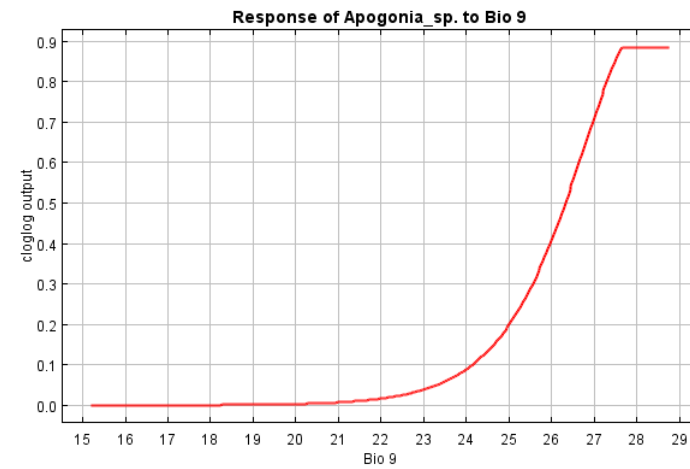
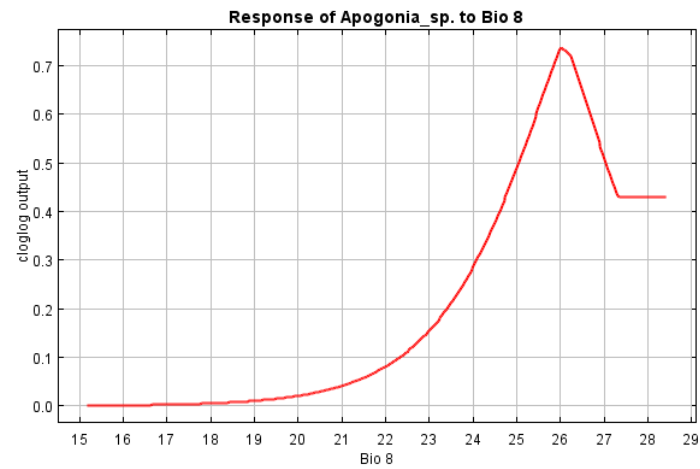
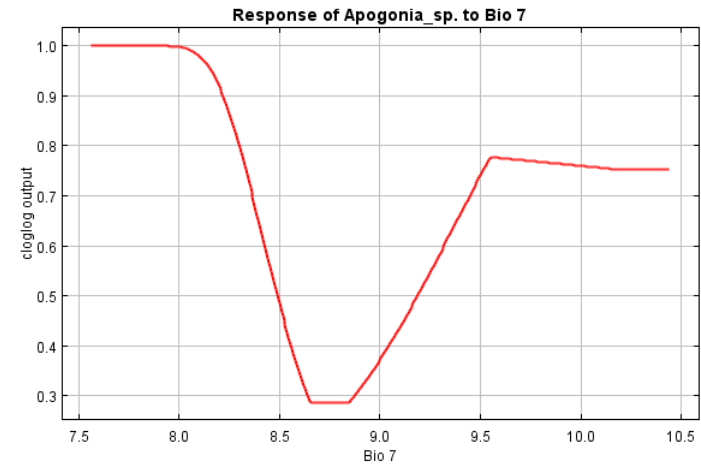
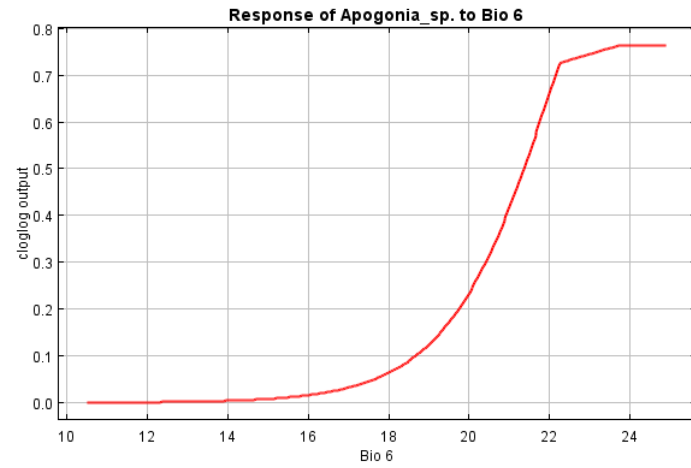
Response curves of MaxEnt model for *Apogonia* spp.

Appendix H



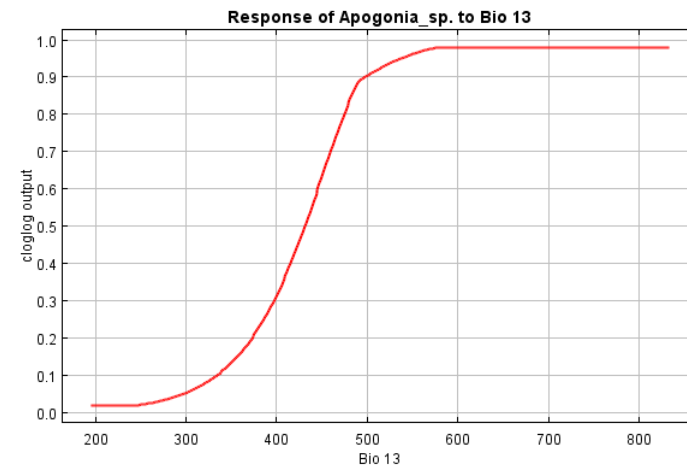
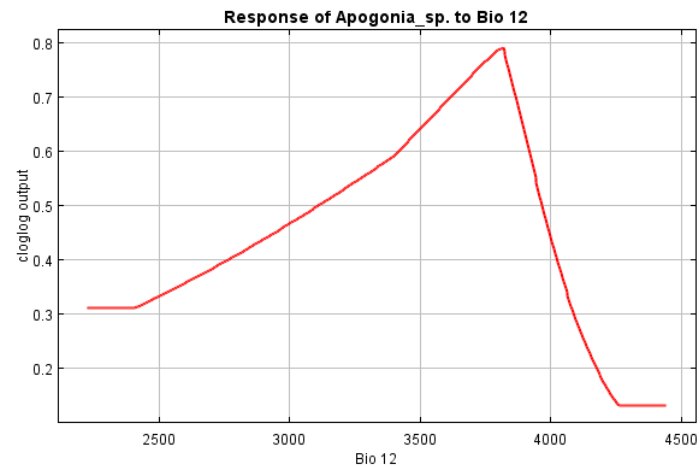
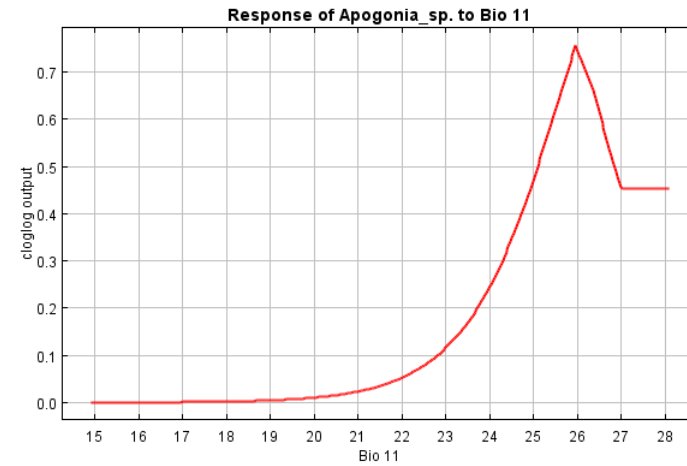
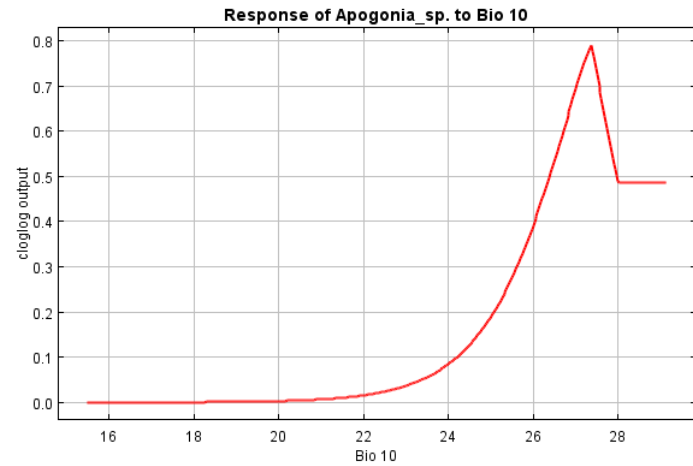
Response curves of MaxEnt model for *Apogonia* spp. using only corresponding variables.

Appendix H continued



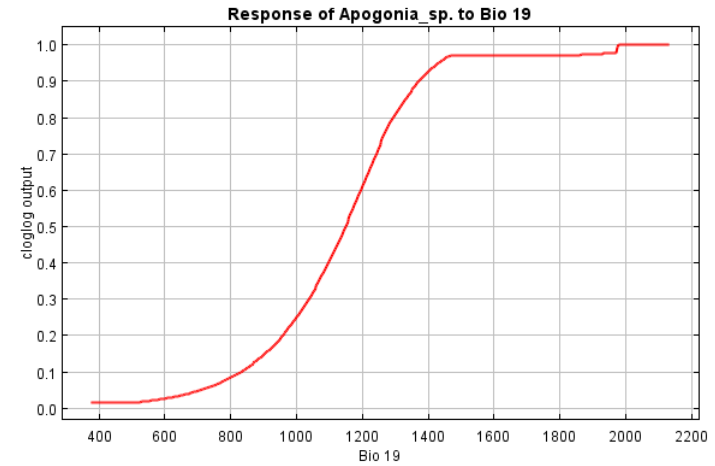
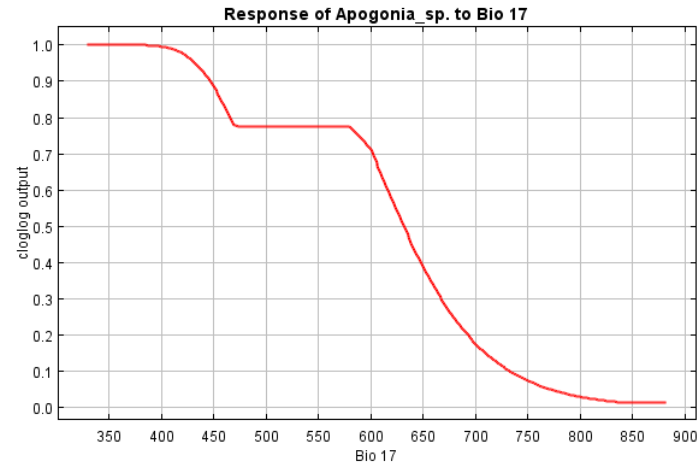
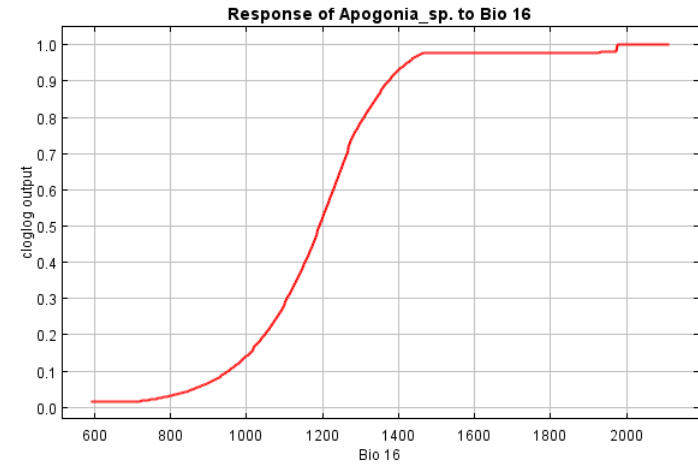
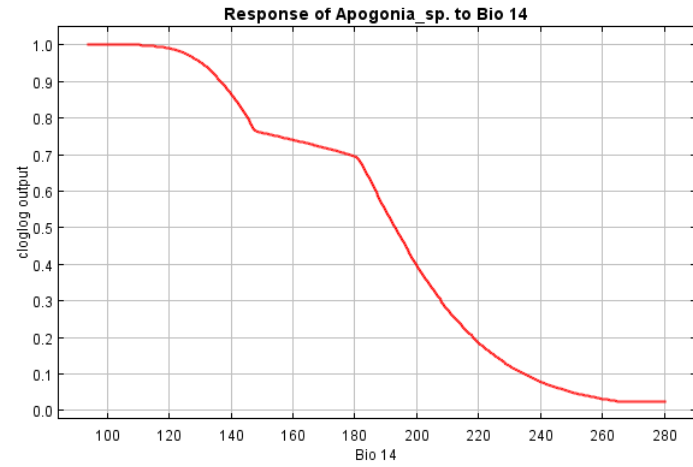
Response curves of MaxEnt model for *Apogonia* spp. using only corresponding variables.

Appendix H continued



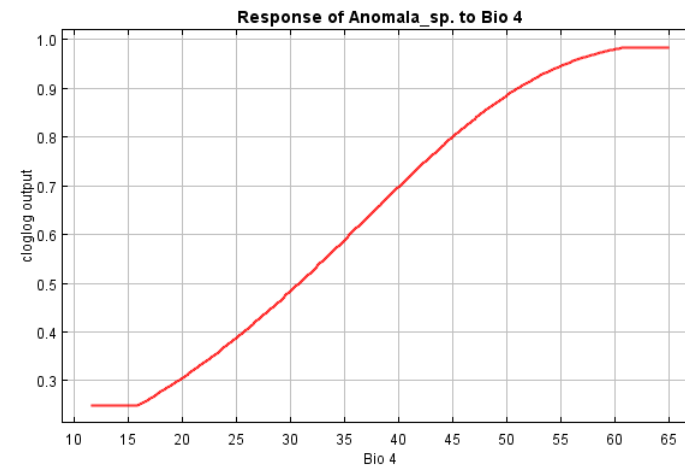
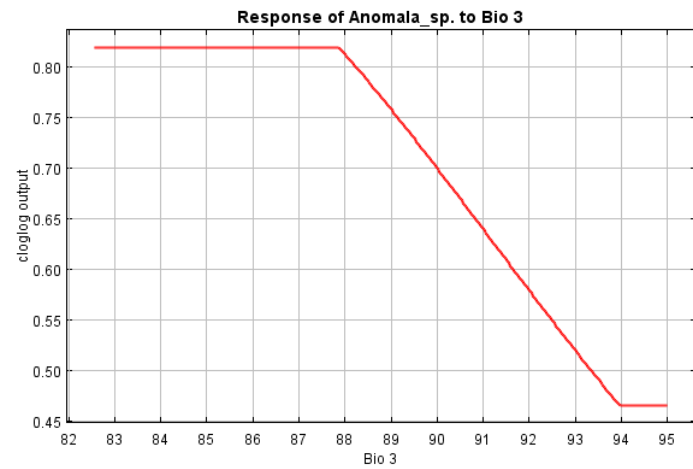
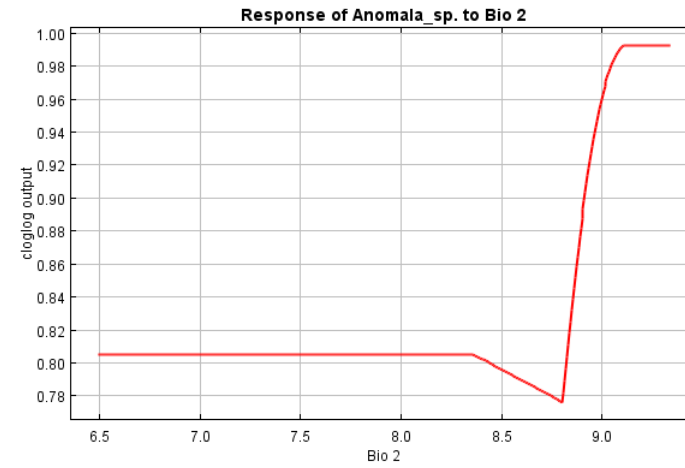
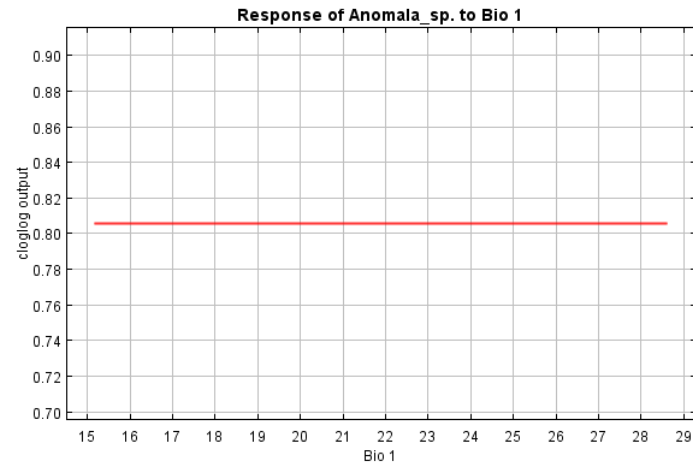
Response curves of MaxEnt model for *Apogonia* spp. using only corresponding variables.

Appendix H continued



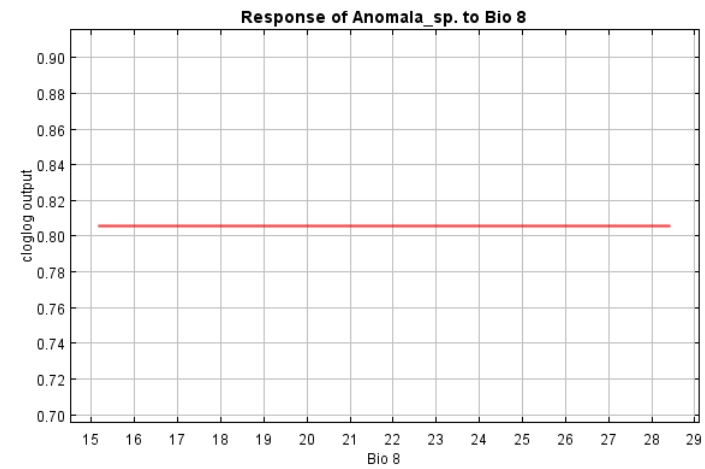
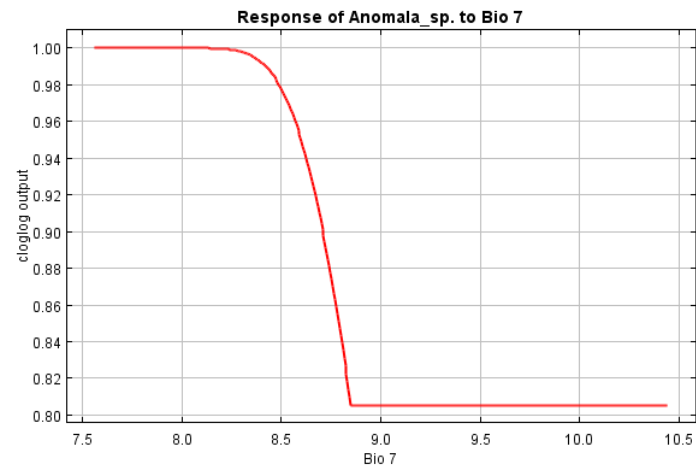
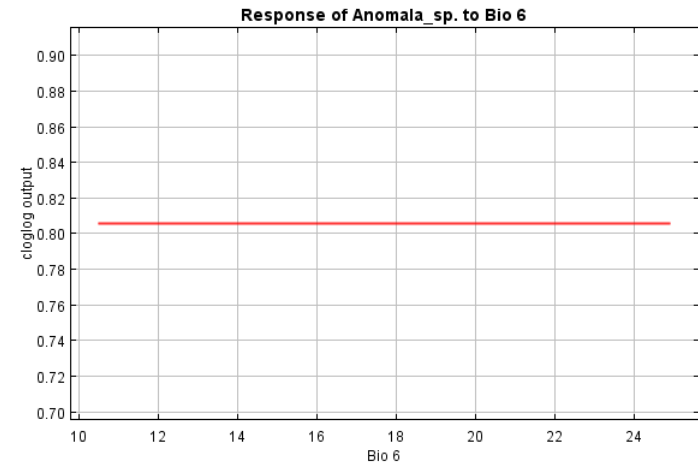
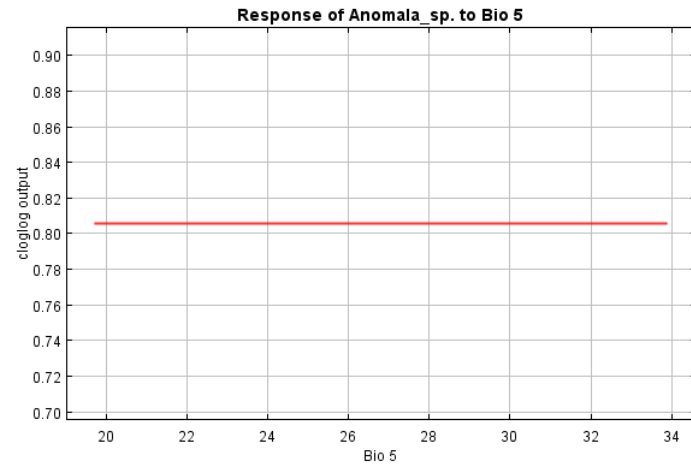
Response curves of MaxEnt model for *Apogonia* spp. using only corresponding variables.

Appendix I



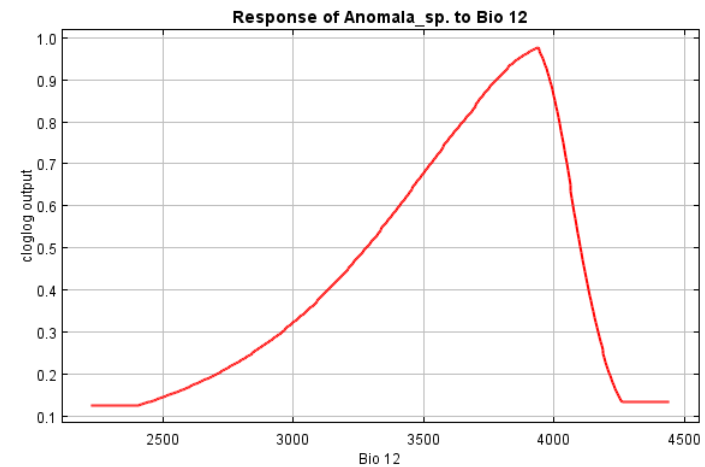
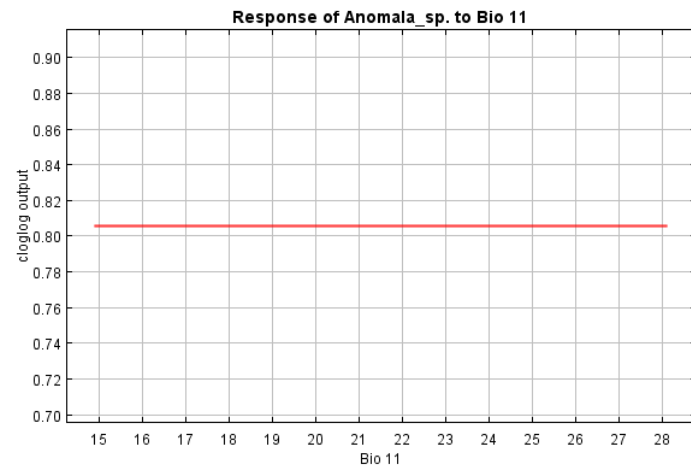
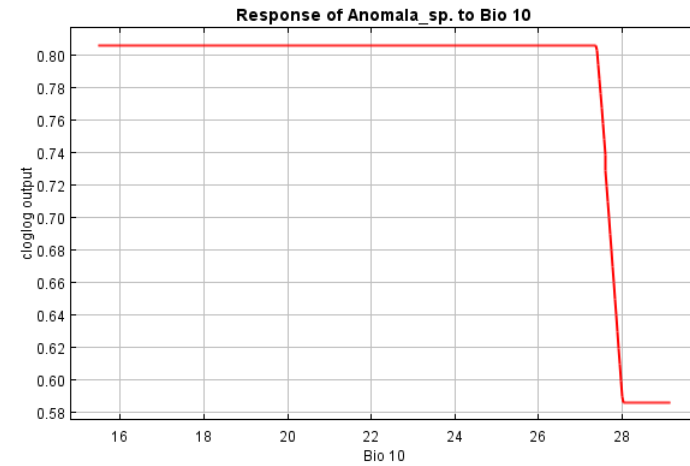
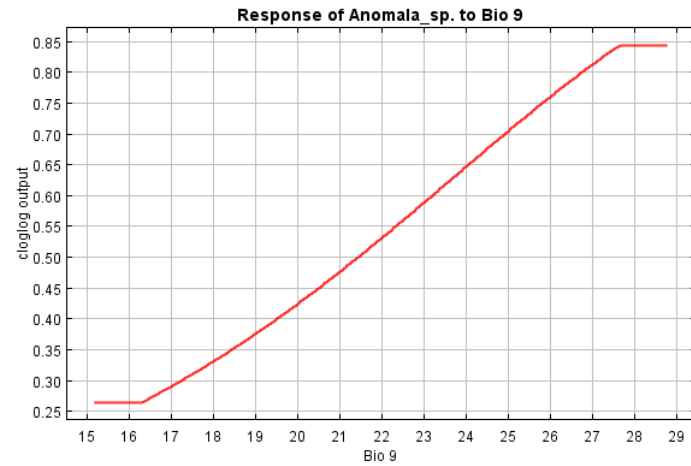
Response curves of MaxEnt model for *Anomala* spp.

Appendix I continued



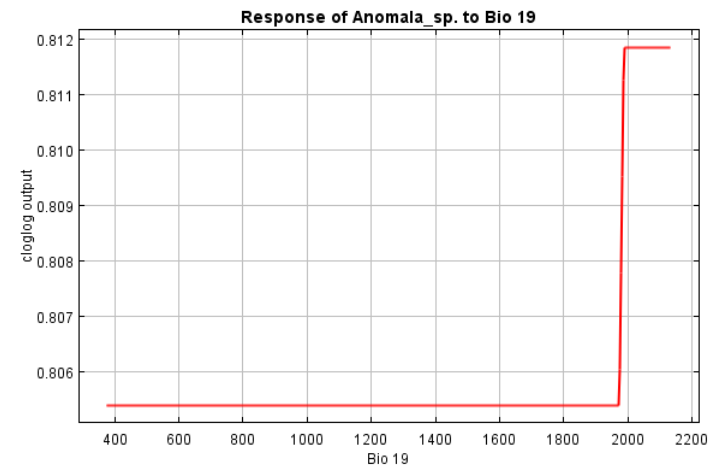
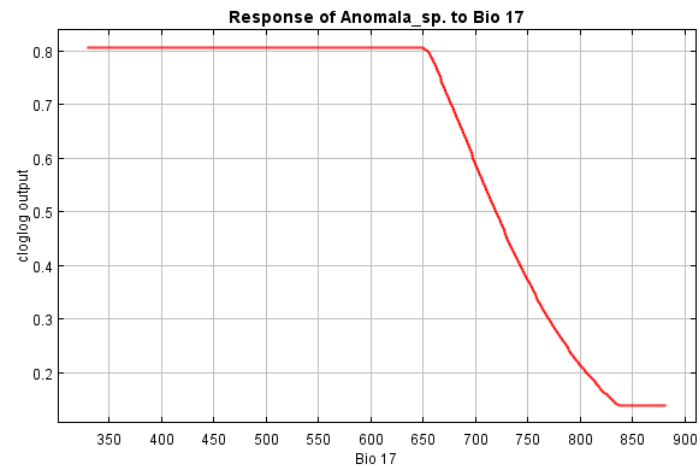
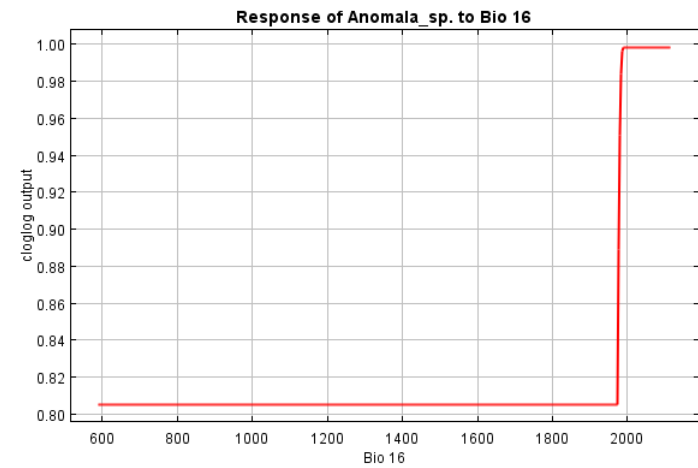
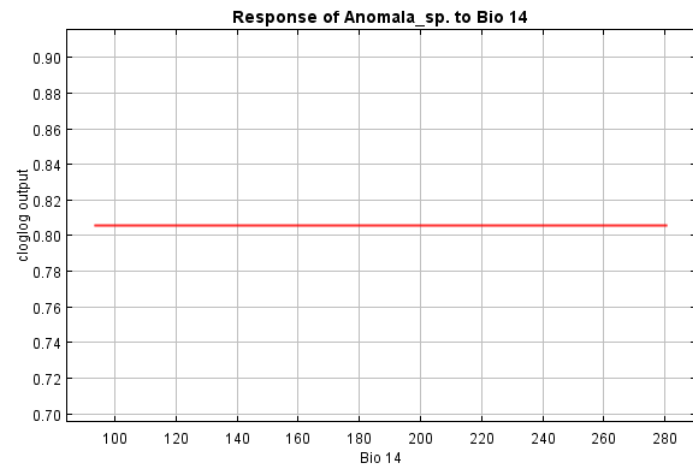
Response curves of MaxEnt model for *Anomala* spp.

Appendix I continued



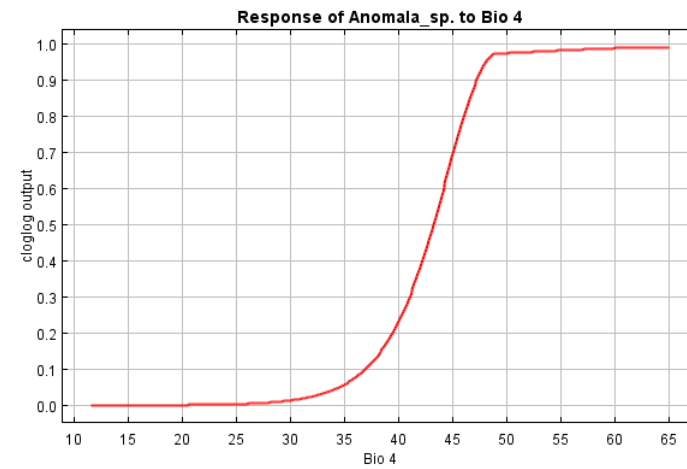
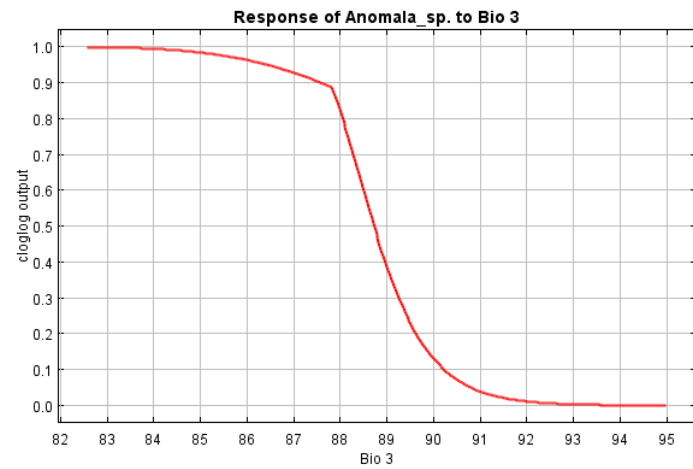
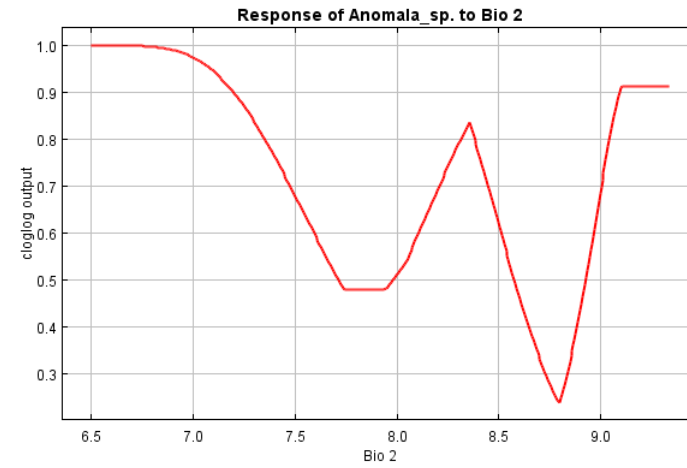
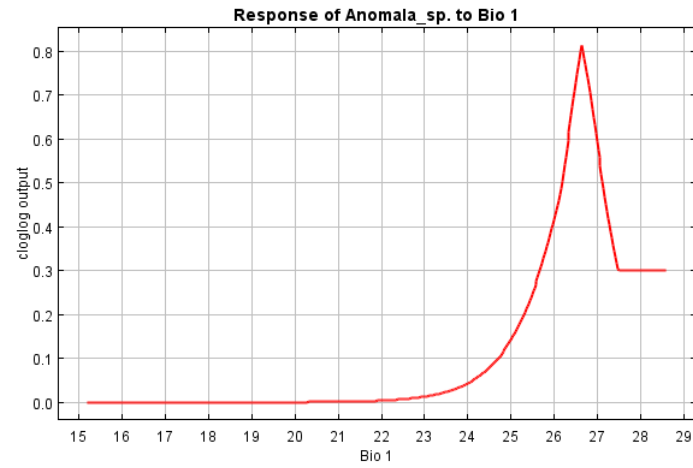
Response curves of MaxEnt model for *Anomala* spp.

Appendix I continued



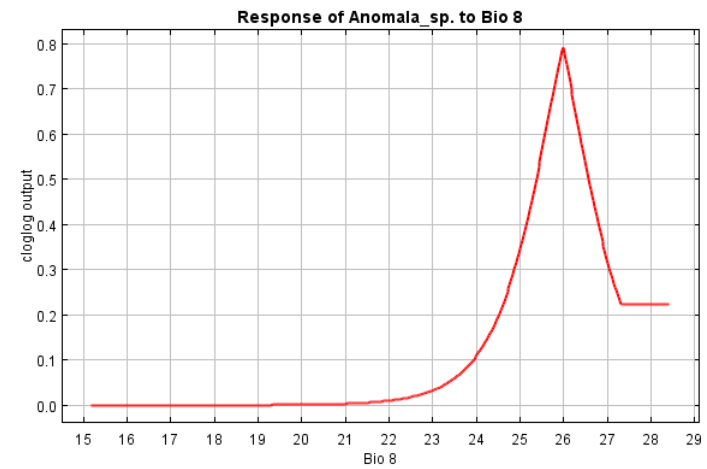
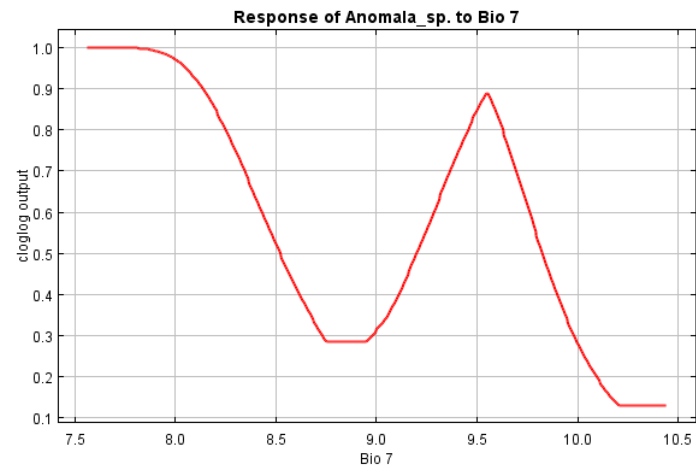
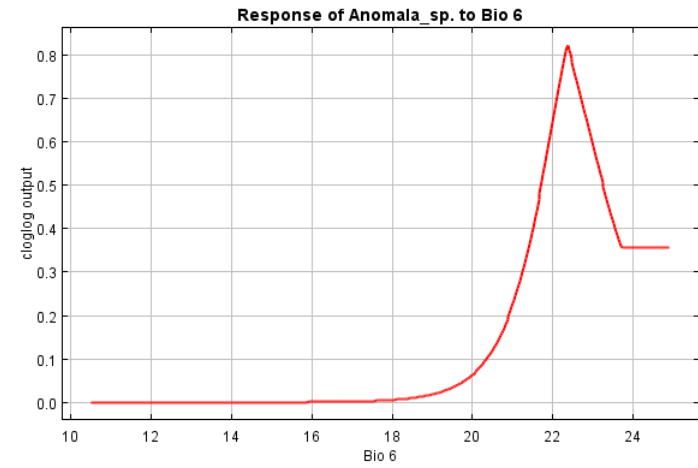
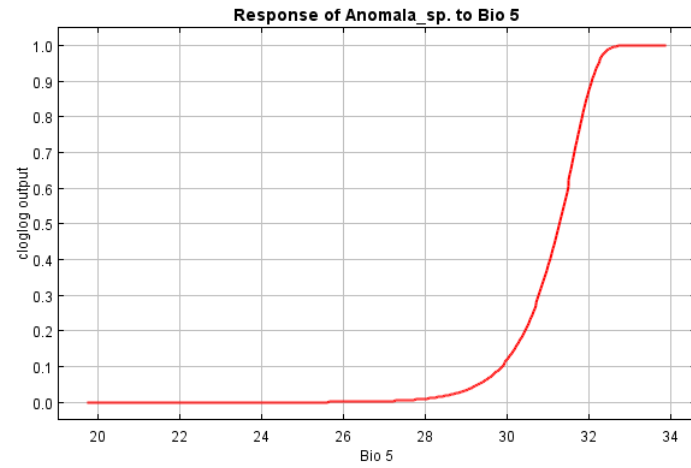
Response curves of MaxEnt model for *Anomala* spp.

Appendix J



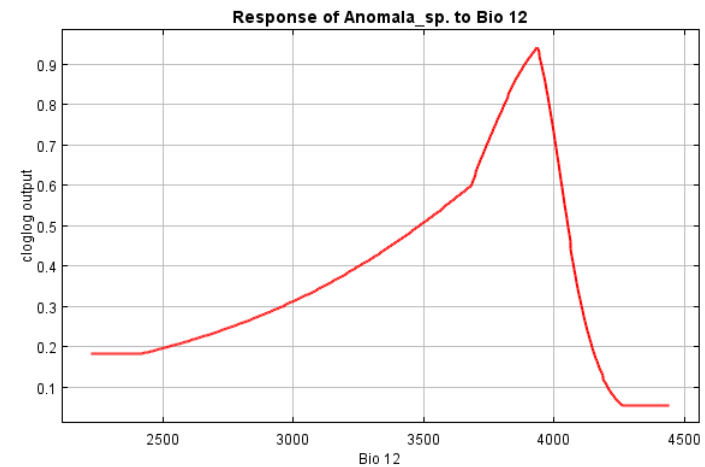
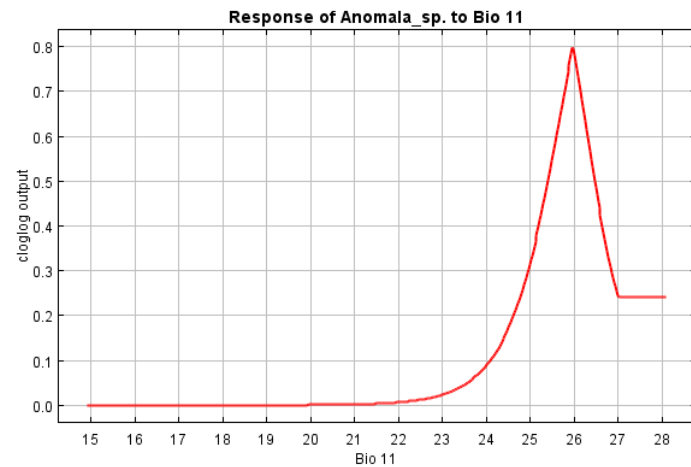
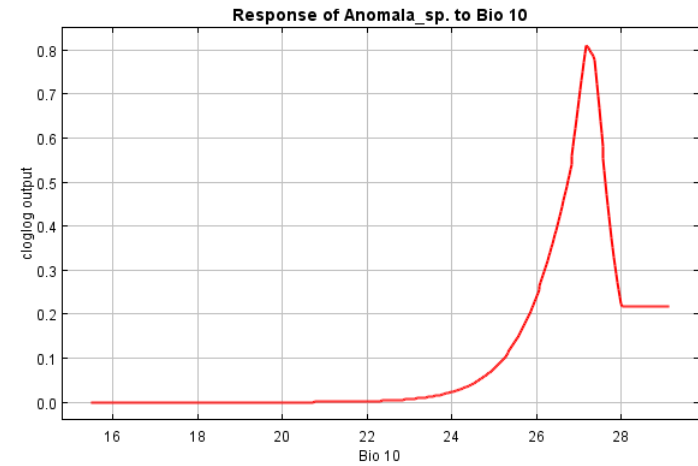
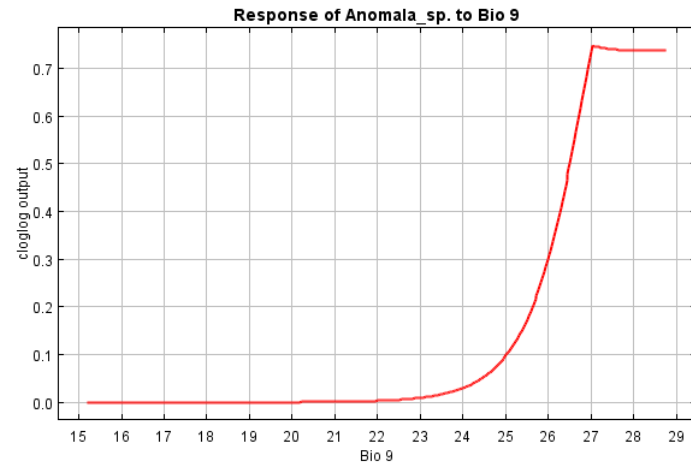
Response curves of MaxEnt model for *Anomala* spp. using only corresponding variables.

Appendix J continued



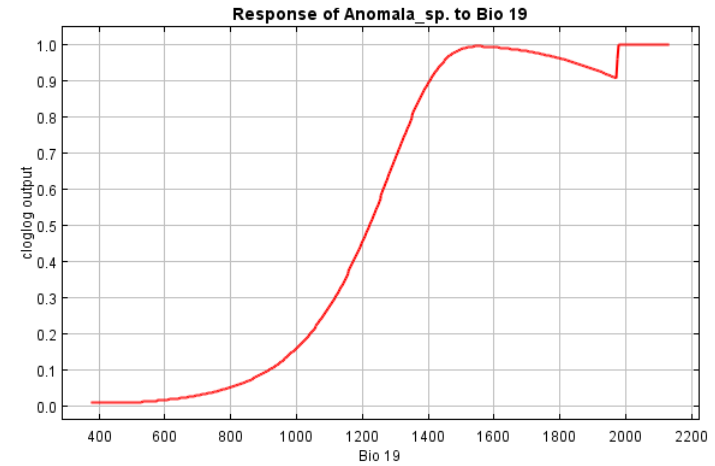
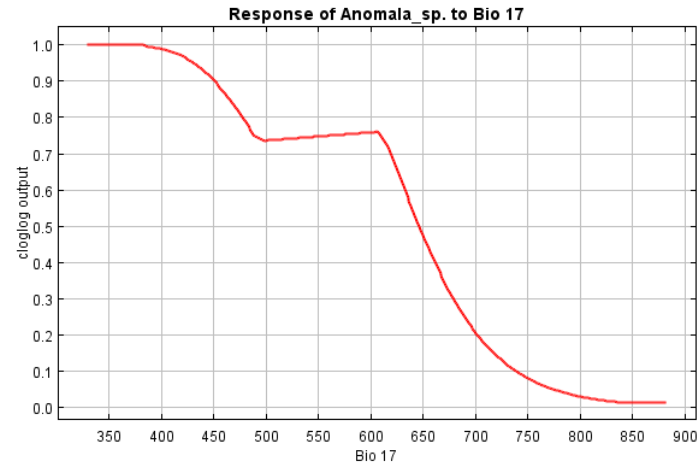
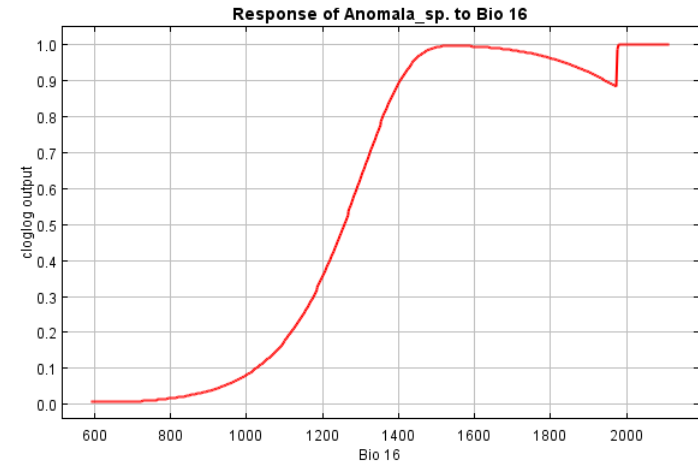
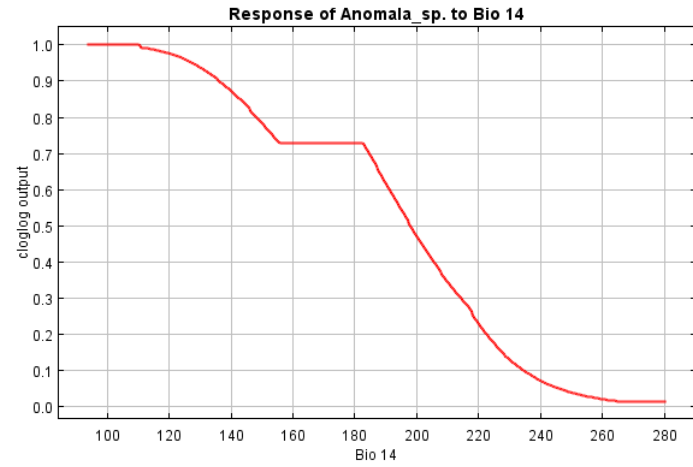
Response curves of MaxEnt model for *Anomala* spp. using only corresponding variables.

Appendix J continued



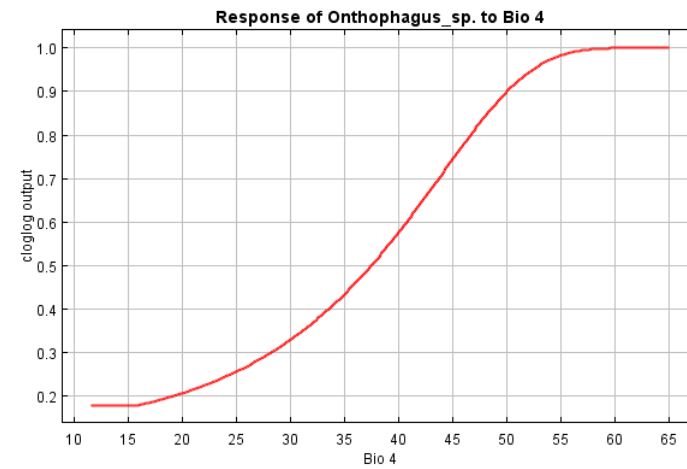
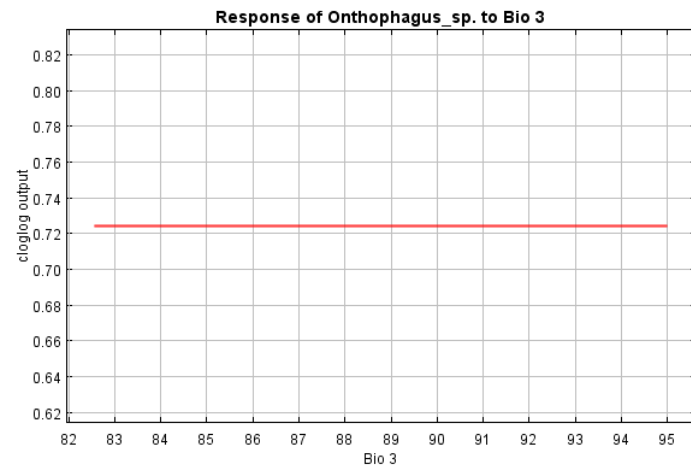
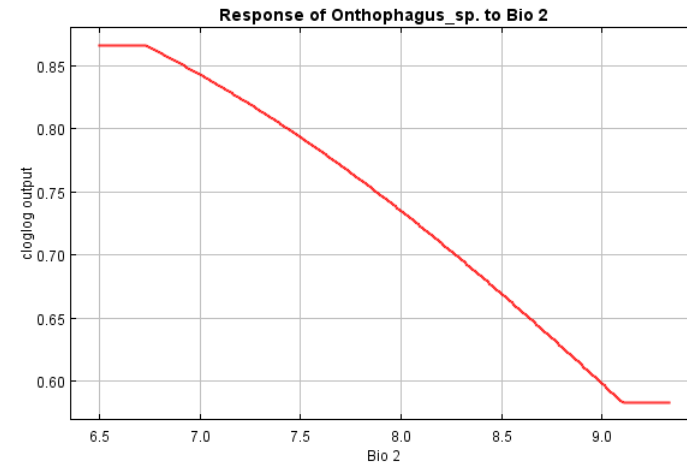
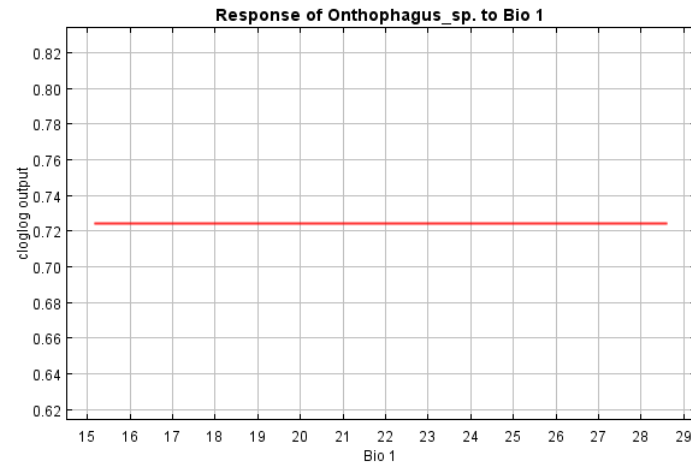
Response curves of MaxEnt model for *Anomala* spp. using only corresponding variables.

Appendix J continued



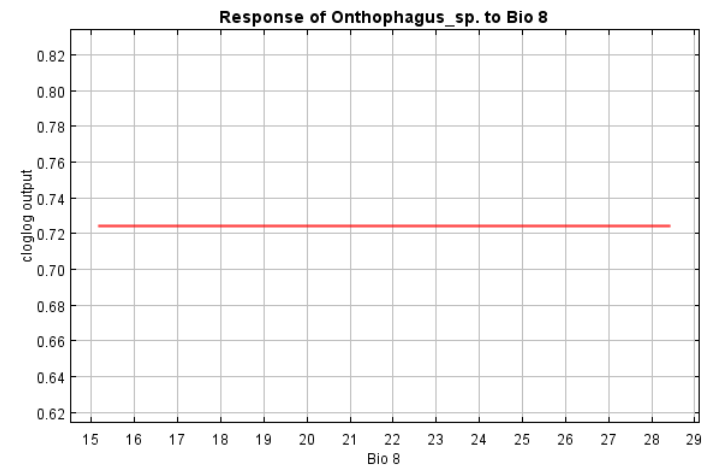
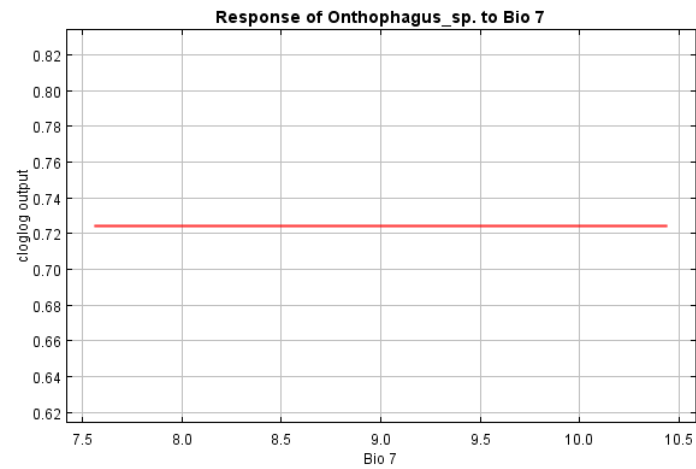
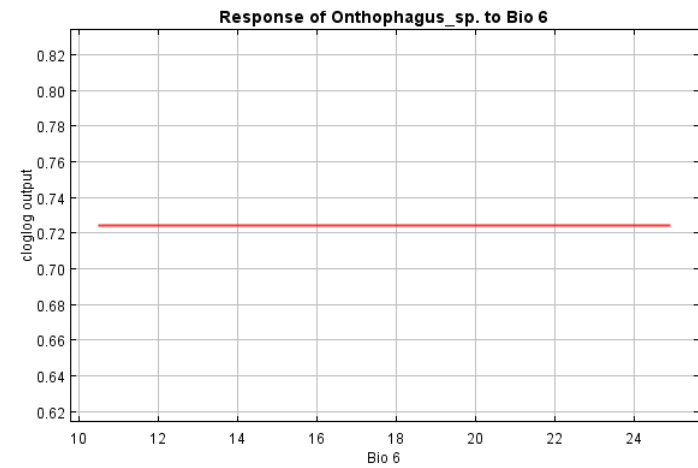
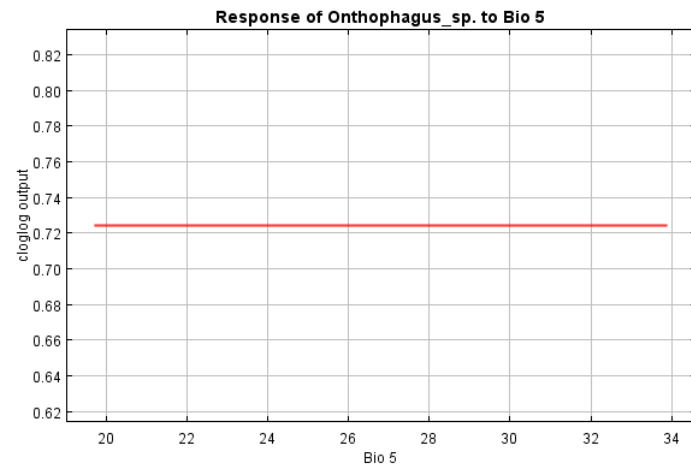
Response curves of MaxEnt model for *Anomala* spp. using only corresponding variables.

Appendix K



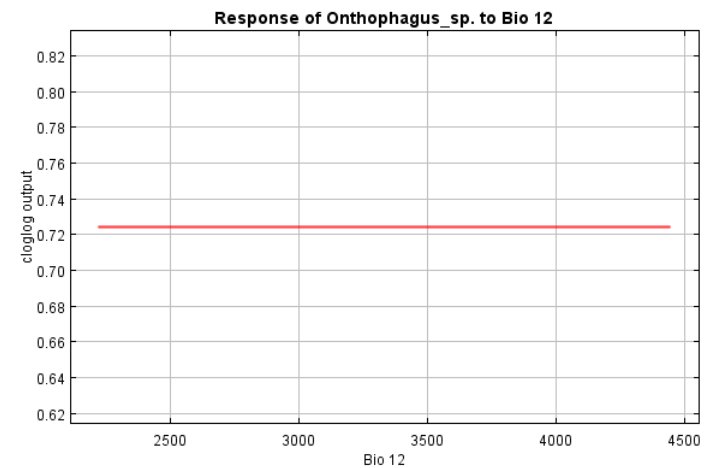
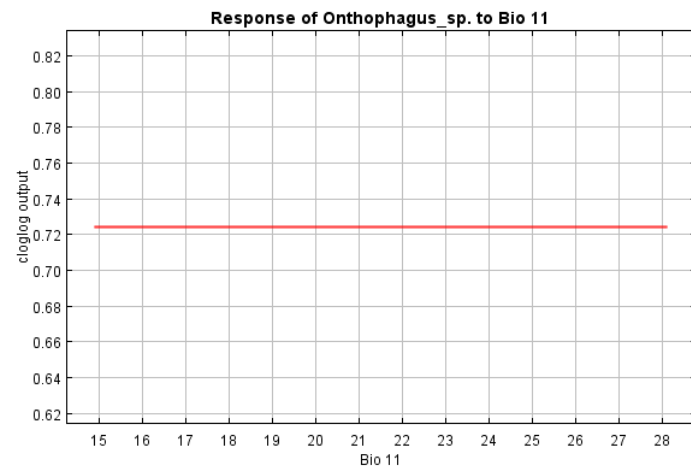
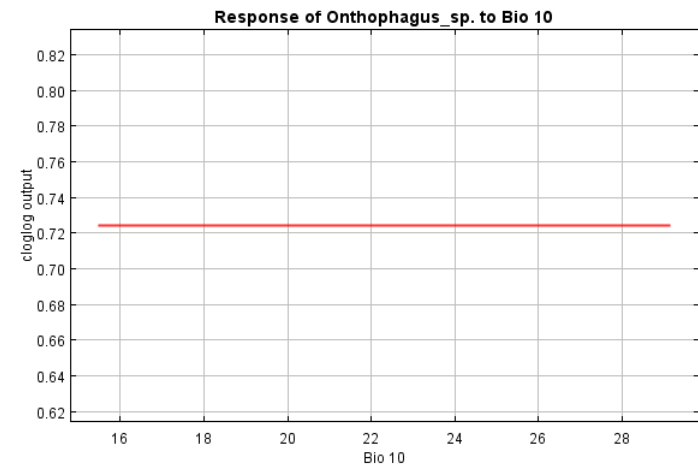
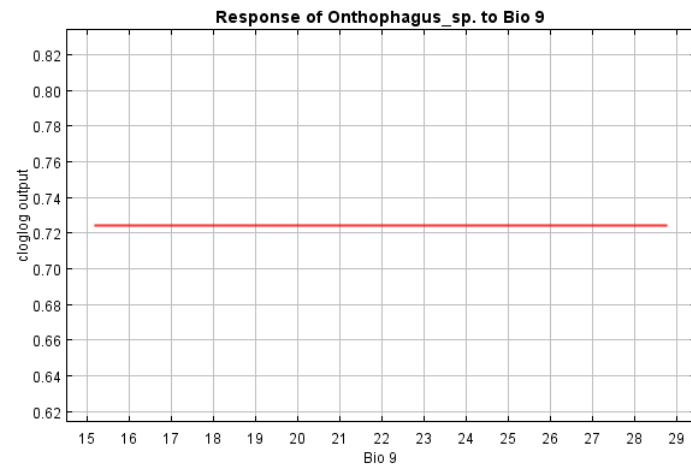
Response curves of MaxEnt model for *Onthophagus* spp.

Appendix K continued



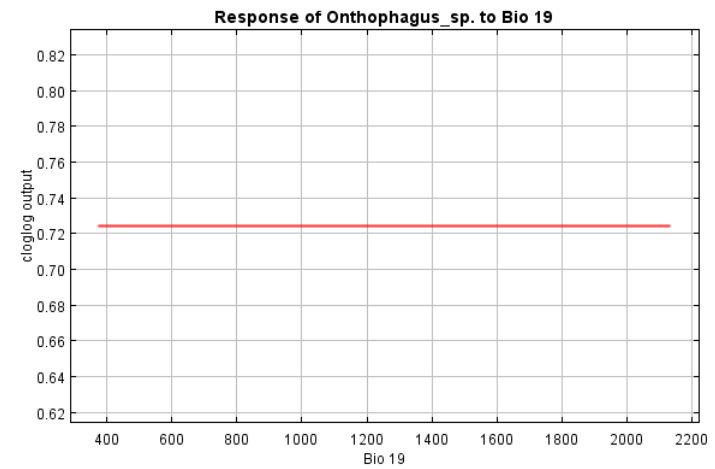
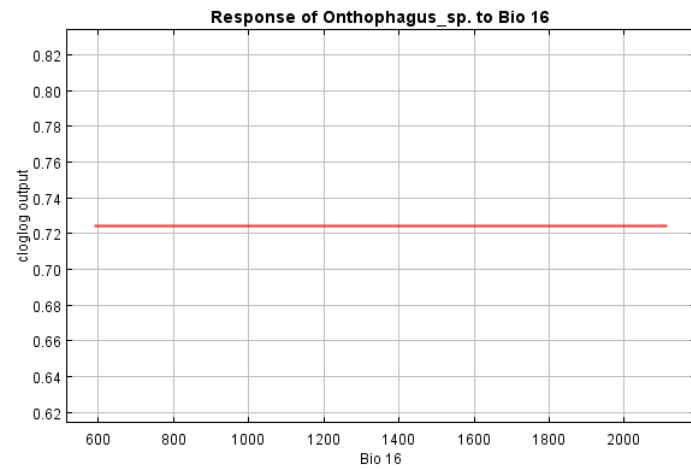
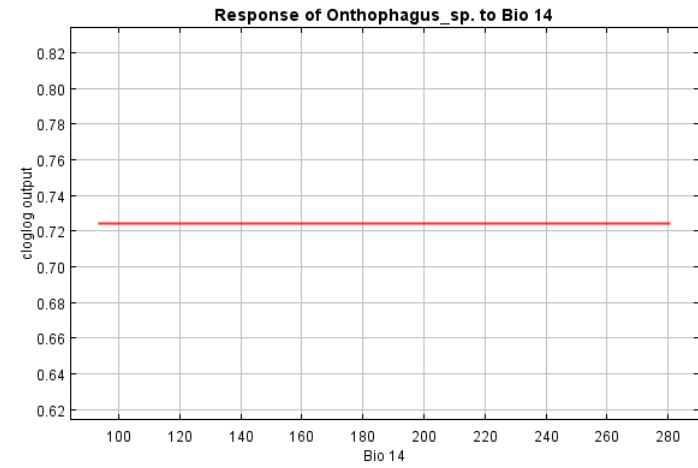
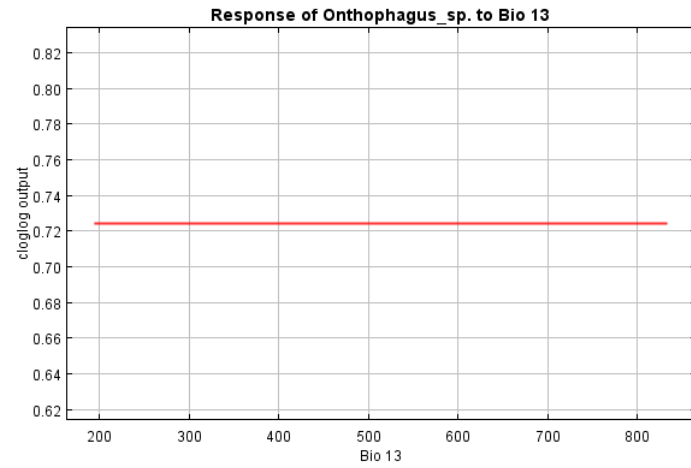
Response curves of MaxEnt model for *Onthophagus* spp.

Appendix K continued



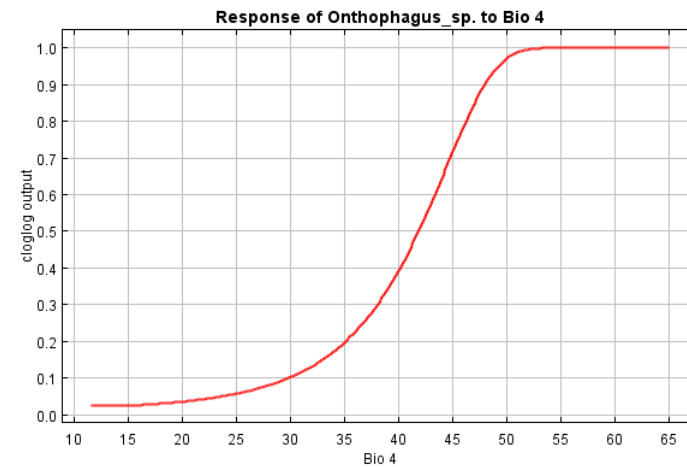
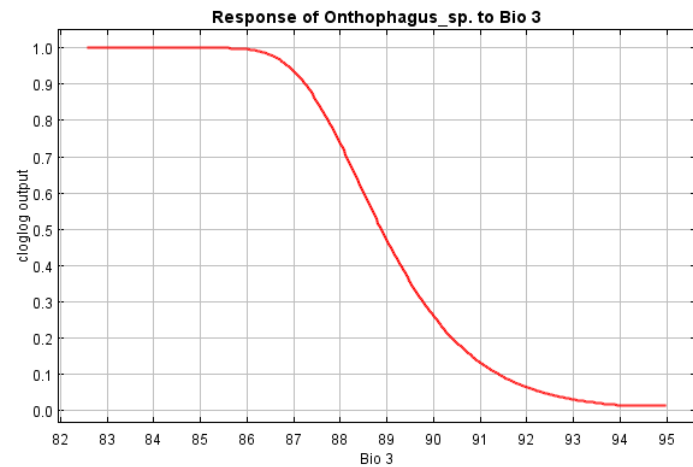
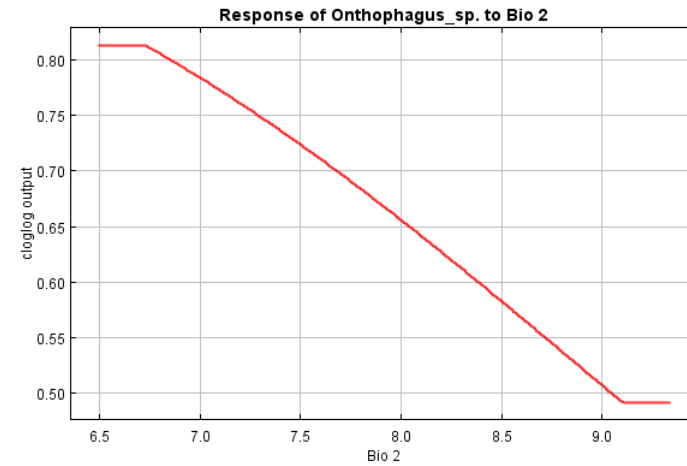
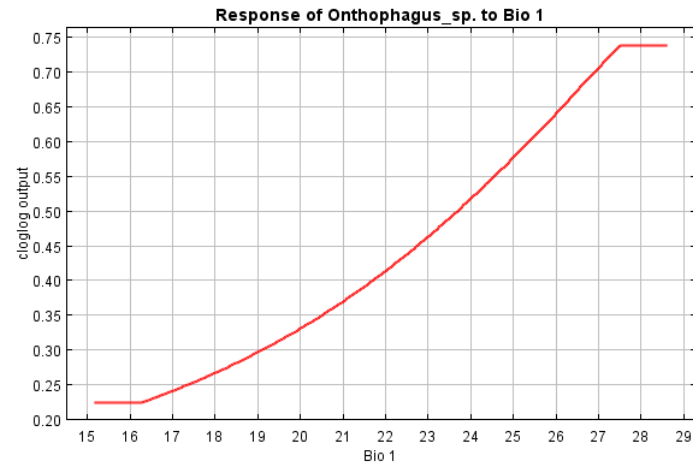
Response curves of MaxEnt model for *Onthophagus* spp.

Appendix K continued



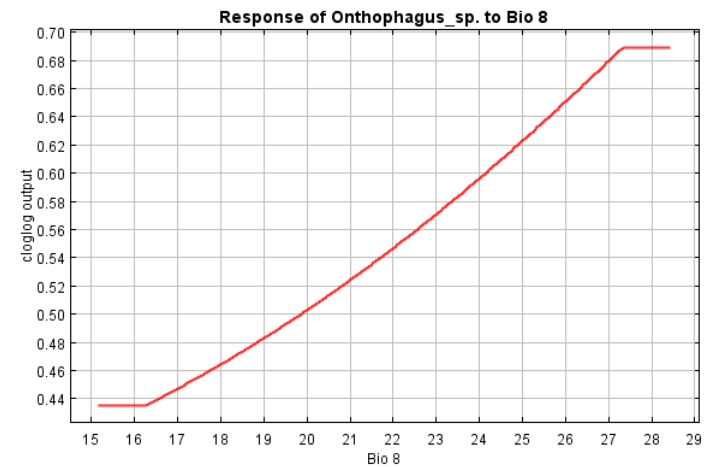
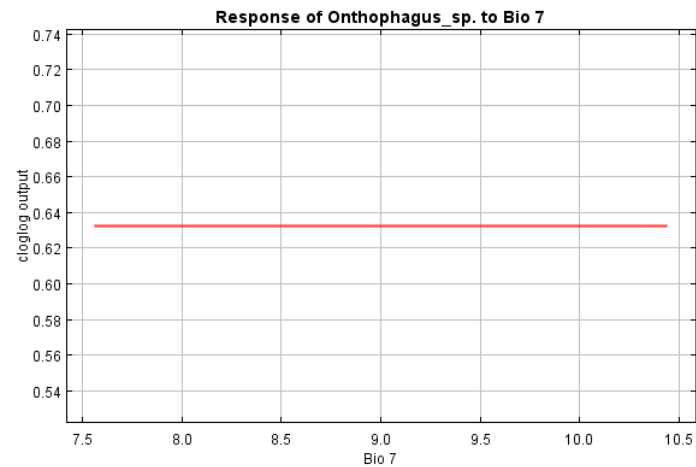
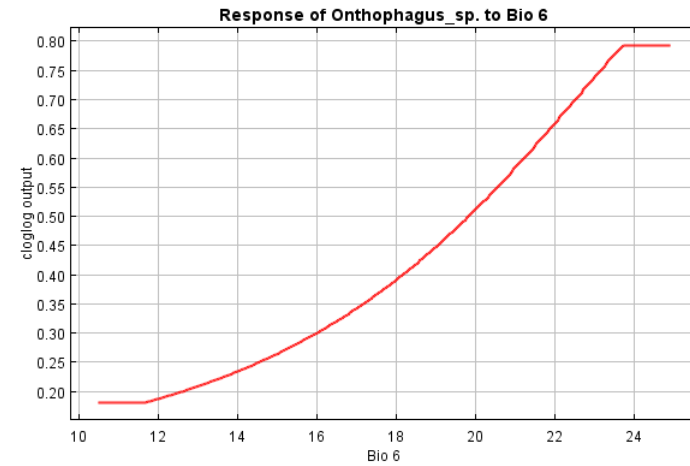
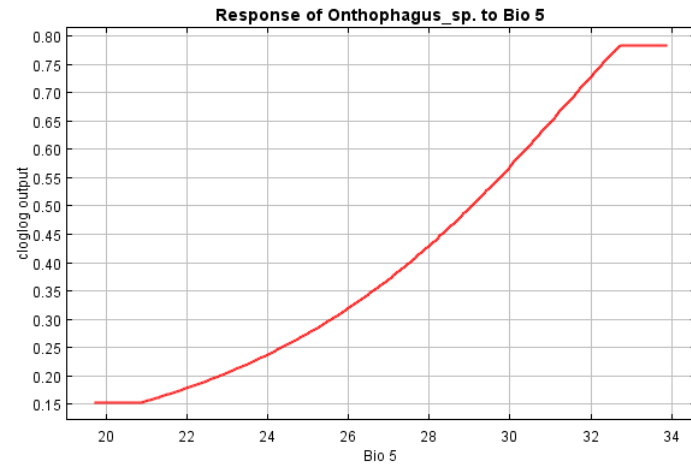
Response curves of MaxEnt model for *Onthophagus* spp.

Appendix L



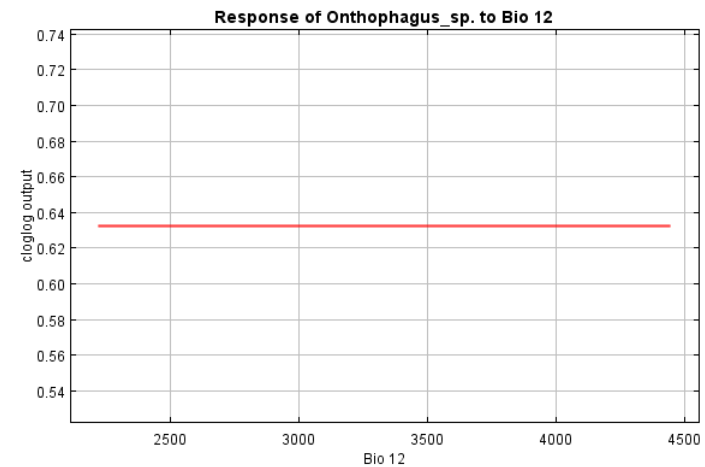
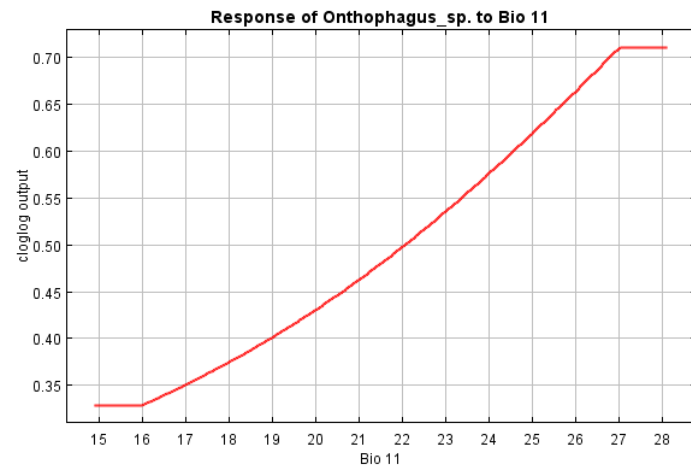
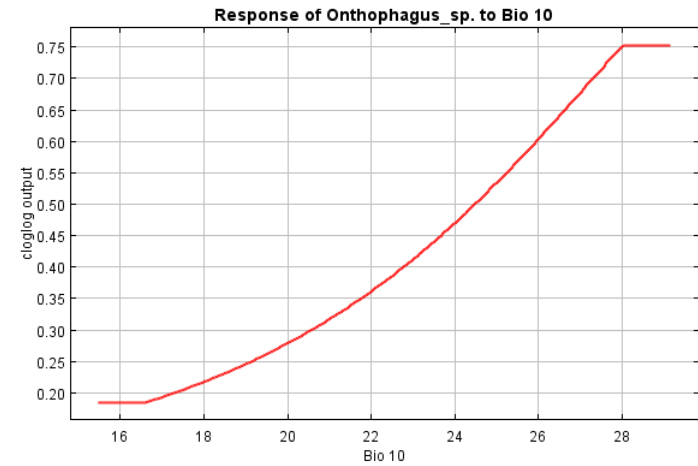
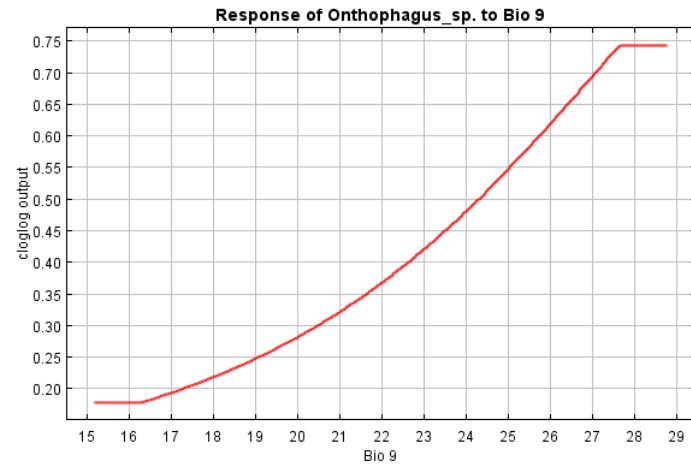
Response curves of MaxEnt model for *Onthophagus* spp. using corresponding variables.

Appendix L continued



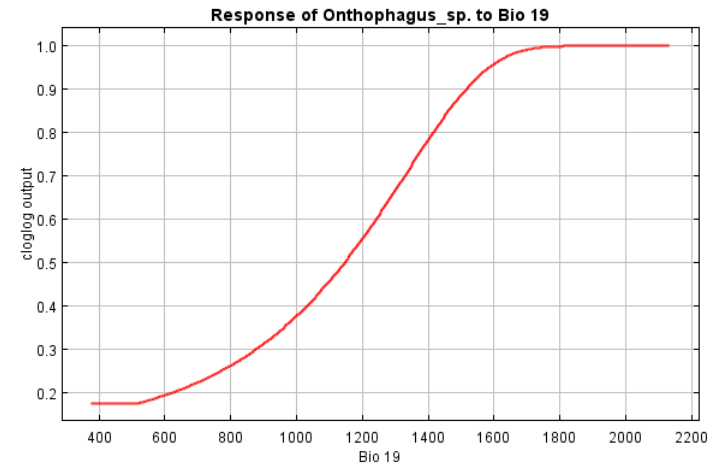
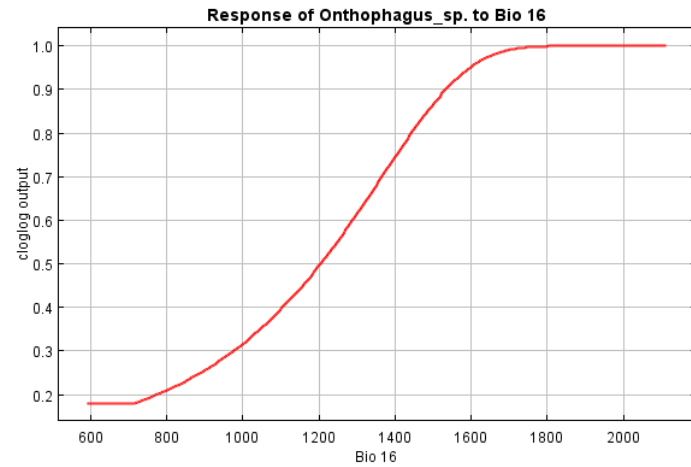
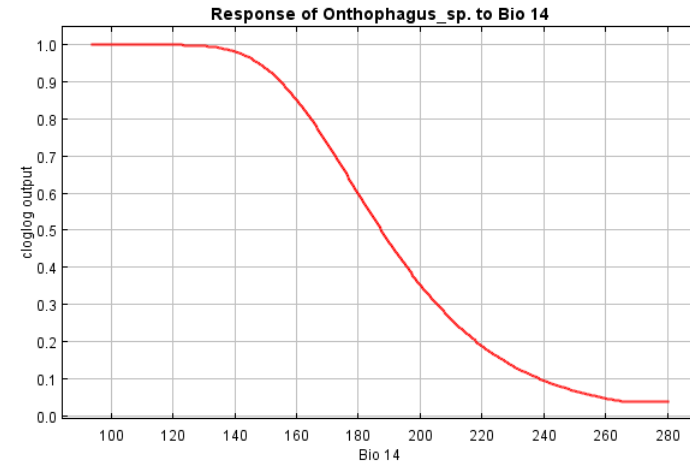
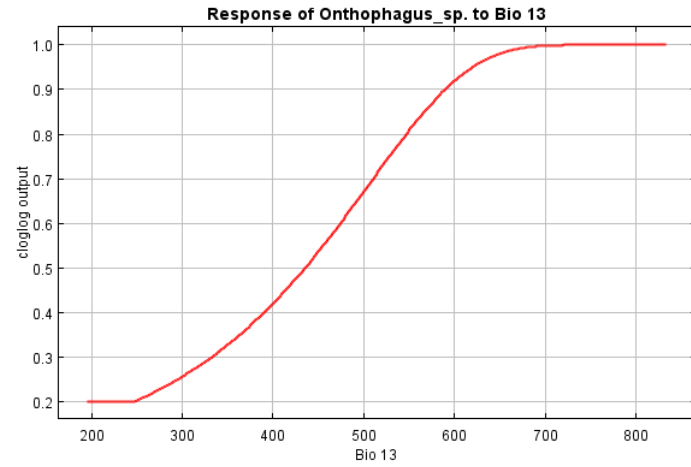
Response curves of MaxEnt model for *Onthophagus* spp. using corresponding variables.

Appendix L continued



Response curves of MaxEnt model for *Onthophagus* spp. using corresponding variables.

Appendix L continued



Response curves of MaxEnt model for *Onthophagus* spp. using corresponding variables.

