INVASION ECOLOGY OF A TROPICAL FERN (*Pneumatopteris afra* (CHRIST.) HOLTTUM) IN NIGERIA: DEVELOPING PREDICTIVE SPATIAL MODEL

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2020

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by

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Thesis submitted in fulfilment of the requirements
for the degree of
Doctor of Philosophy

November 2020

ACKNOWLEDGEMENT

My foremost appreciation goes to the Almighty God who loves me, gave me eternal life, strength, and wisdom to complete this PhD thesis. I want to express my profound gratitude to my Supervisor, Associate Prof. Rahmad Bin Zakaria for his patience, immense supports, encouragements, and supervision from the beginning of my application for admission into the Universiti Sains Malaysia till the end of this study. May the almighty God reward his kindness and consistent supports towards me. I am greatly indebted to my sweetheart, Mrs Rebecca Akomolafe and my lovely children (Victory and Mighty Akomolafe). I am forever grateful to them for their sacrifices in allowing me to travel abroad for this study. I wouldn't have been able to complete this study without the prayers and supports of my wife, who stood in the gap for me and took care of the home while I was away.

The following academic mentors and advisors have made positive impacts on life during my academic journey; Associate Prof. Oloyede Fatai (My B.Sc. and M.Sc. degrees supervisor), Prof. E.A. Odu, Prof. A.M. Makinde, Prof. Isichei A., Prof. E.H. Kwon_Ndung, Prof. Makinde S.C.O., Prof. Agboola D.A. and Prof. Adedeji O. I will not forget to appreciate my parents, Mr. and Mrs Akomolafe Josiah who have sacrificed a lot for my upbringing. I also acknowledge my spiritual father, Pastor E.B. Olukomogbon, for his persistent prayers and encouragements. I also extend my acknowledgement to my colleagues in the Department of Botany, Federal University of Lafia (Mr Terna Paul, Mr Mshelmbula Barka, Mr Goler, Mr Okogbaa James and Mr Bello). Special thanks to Dr Shomboro Karau, who introduced me to the modelling techniques. Finally, I appreciate the management of the Federal University of Lafia for nominating me for the PhD study fellowship and the Nigerian Tertiary Education Trust Fund (TETFund) for providing the financial support for this study.

May the Almighty God continue to bless and support you all.

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LIST OF ABBREVIATIONS

AAS	Atomic Absorption Spectrophotometer
ANNs	Artificial Neural Networks
ANOVA	Analysis of Variance
AP	Available Phosphorus
AUC	Area Under the Curve
BD	Bulk Density
BS	Base Saturation
CCA	Canonical Correspondence Analysis
CEC	Cation Exchange Capacity
Cont’d	Continued
DMRT	Duncan Multiple Range Test
EA	Exchangeable Acidity
ENMs	Ecological Niche Models
GARP	Genetic Algorithm for Rule-set Production
GBIF	Global Biodiversity Information Facility
GIS	Geographical Information System
GLM	Generalized Linear Models
GPS	Global Positioning System
HC	Hydraulic Conductivity
IAP	Invasive Alien Plants
IAS	Invasive Alien Species
IPNI	International Plant Names Index
ITV	Intraspecific Trait Variability
IUCN	International Union of Conservation of Nature
LDMC	Leaf Dry Matter Content
MAXENT	Maximum Entropy
MC	Moisture Content
N	Normality
OC	Organic Carbon
OM	Organic Matter
PCA	Principal Component Analysis
ROS	Receiver Operating Characteristics

SDMs	Species Distribution Models
SDMC	Stipe Dry Matter Content
SDT	Stipe Drying Time
SLA	Specific Leaf Area
SPSS	Statistical Package for Social Sciences
SVMs	Support Vector Machines
TP	Total Porosity
USD	United States Dollars
USGS	United States Geological Survey
VIF	Variance Inflation Factor

EKOLOGI PENCEROBOHAN PAKU PAKIS TROPIKA (***Pneumatopteris afra*** (CHRIST.) HOLTTUM) DI NIGERIA: MEREKABENTUK MODEL RUANGAN PREDIKTIF

ABSTRAK

Pencerobohan tanah lembap oleh *Pneumatopteris afra* di sebahagian kawasan di Lafia, Nigeria memberi ancaman kepada tanah lembap dengan mengurangkan jumlah penembusan cahaya dan menghalang aliran air. Oleh itu, kajian ini bertujuan untuk membina model ramalan ruangan berkenaan taburan *P. afra* dan menggunakan pendekatan sifat-sifat berfungsi bagi memperoleh pemahaman mekanistik terhadap dinamik komuniti dan ciri-ciri ekosistem tanah lembap yang menyerang dan tidak menyerang. Enam bidang tanah lembap dipilih yang terdiri daripada tiga bidang tapak yang telah menyerang dan tiga bidang tapak yang tidak menyerang di Lafia, Nigeria. Setiap tapak mempunyai keluasan 500 × 500 m yang telah ditentukan untuk kajian ini. Data kewujudan *P. afra* di setiap tapak yang dikolonisasi diperoleh. Data tersebut yang digandingkan dengan pemboleh ubah bioiklim digunakan untuk membina model ramalan *maxent* berkenaan taburan *P. afra* di Lafia dan keseluruhan Nigeria. Kelimpahan setiap spesies tumbuhan dan indeks kepelbagaian dianggarkan menggunakan 40 kuadran yang diletakkan pada jarak 10 m di empat buah rentasan sepanjang 200 m di setiap tanah lembap. Sifat-sifat berfungsi *P. afra* di tapak yang diceroboh juga dinilai. Parameter fizikal (termasuk pH, tekstur, ketumpatan pukal, dan keliangan) dan kimia (termasuk kandungan nitrogen, natrium, dan kalium) tanah di setiap tapak ditentukan. Hasil pemodelan ramalan di seluruh Nigeria menunjukkan bahawa *P. afra* dipengaruhi oleh min suhu tahunan, min suhu sukuan paling kering, kebermusiman kerpasan, kerpasan sukuan paling kering dan kerpasan sukuan paling sejuk. Jumlah kawasan yang dijangka akan terkesan pada masa hadapan ialah 26,019.11 km^2 merentasi empat negeri di Nigeria. *P. afra* mempunyai kekerapan relatif dan kelimpahan tertinggi di semua tapak yang diceroboh dengan lebih 80% liputan. Kelimpahan *P. afra* juga menunjukkan korelasi negative dengan indeks kepelbagaian (H′ = -0.741, indeks Simpson = -0.518, keseimbangan = -0.707). Tapak yang tidak menyerang menunjukkan kepelbagaian (H′ = 2.252, indeks Simpson = 0.877) dan kekayaan (14) jauh lebih tinggi berbanding tapak yang diserang (H′ = 0.618, indeks Simpson = 0.237, kekayaan = 9). Penilaian sifat-sifat berfungsi menunjukkan *P. afra* memanfaatkan berat daun segar, ketinggian tumbuhan, bilangan daun, kandungan bahan daun kering dan keluasan tertentu daun sebagai faktor di semua tapak. Sifat-sifat ini merupakan petunjuk kepada keupayaan kompetitif yang tinggi, kemudahterbakaran yang rendah dan perolehan sumber yang cekap. Penilaian tanah juga menunjukkan bahawa *P. afra* lebih suka tanah dengan pH yang rendah (3.22), kekonduksian hidraulik yang rendah (1.23 cm^3) dan kandungan nitrogen yang rendah (0.08%). Sebagai kesimpulan, *P. afra* menunjukkan kecenderungan untuk menjadi sangat invasif sekiranya tidak dikawal lebih awal. Pengetahuan berkenaan faktor persekitaran dan fisiologi boleh dimanfaatkan dalam pengurusan dan pengawalan tumbuhan ini. Ini akan menyelamatkan tanah lembap daripada ancaman penyebaran pada masa hadapan.

INVASION ECOLOGY OF A TROPICAL FERN (*Pneumatopteris afra* (CHRIST.) HOLTTUM) IN NIGERIA: DEVELOPING PREDICTIVE SPATIAL MODEL

ABSTRACT

The invasion of wetlands by *Pneumatopteris afra* in some parts of Lafia, Nigeria has posed threats to the wetlands by reducing the amount of light penetration and hindering water flow. Therefore, this study aims at building a predictive spatial model of distribution of *P. afra* and use functional traits approach to obtain a mechanistic understanding of the community dynamics and ecosystem properties of invaded and non-invaded wetlands. Six wetlands were chosen, consisting of three invaded and three non-invaded sites in Lafia, Nigeria. Each site has an area of 500 m x 500 m demarcated for the study. The occurrence data of *P. afra* at each invaded site was obtained. This data, coupled with bioclimatic variables, were used to build a maxent predictive model of distribution of *P. afra* in Lafia and entire Nigeria. The abundance of each plant species and diversity indices were estimated using forty quadrants laid at 10m intervals across four 200m transects at each wetland. The functional traits of *P. afra* at the invaded sites were also assessed. The soil physical (including pH, texture, bulk density, and porosity) and chemical (including nitrogen content, sodium, and potassium) parameters of all the sites were determined. The result of the predictive modelling in entire Nigeria revealed that *P. afra* is influenced by annual mean temperature, mean temperature of driest quarter, precipitation seasonality, precipitation of driest quarter and precipitation of coldest quarter. The total predicted area to be affected in the future was found to be 26,019.11 Km^2 across four States of Nigeria. *P. afra* has the highest relative frequency and abundance in all the invaded sites with more than 80% percentage cover. The abundance of *P. afra* also exhibited negative correlations with the diversity indices (H′ = -0.741, Simpson index = -0.518, evenness = -0.707). The non-invaded sites showed significantly higher diversity (H′ = 2.252, Simpson index = 0.877) and richness (14) than the invaded ones (H′ = 0.618, Simpson index = 0.237, richness = 9). The functional traits assessment revealed that *P. afra* utilizes leaf fresh weight, plant height, number of leaves, leaf dry matter content and specific leaf area as its drivers in all the sites. These traits are indicators of its highly competitive ability, low inflammability, and efficient acquisition of resources. Also, the soil assessment showed that *P. afra* prefers soil with low pH (3.22), low hydraulic conductivity (1.23 cm^3) and low nitrogen (0.08%). Conclusively, *P. afra* has demonstrated the tendencies to be highly invasive if not controlled early. This knowledge of its environmental and physiological drivers can be harnessed in its management and control. This will save our wetlands from the menace of its future spread.

CHAPTER 1

INTRODUCTION

1.1 Background of the Study

Biological invasion by alien species is known to be one of the main factors responsible for biodiversity loss and endangered species listings globally (Richardson et al., 2014). The biological invasion has led to an exponential increase in the movement of organisms from one part of the world, thereby causing tremendous damage to the natural ecosystems of the new habitats (Downey and Richardson, 2016; Jansen, 2019; Rejmánek and Richardson, 2013). Invasive plant species are non-native exotic plant species growing in native plant communities (Colautti and MacIsaac, 2004). They are species introduced into new areas that adversely affect the habitats and bioregions they invade economically, environmentally, and ecologically (Mostert et al., 2017; van Wilgen and Richardson, 2014). They can often displace the native plant species by reproducing faster than the natives.

Many alien plants do not have any natural pests or predators in their new habitats; consequently, they have an advantage over the natives by being able to compete better within the same community (Kull et al., 2011; Shackleton et al., 2016). Invasive plants could also be regarded as plants that have shown the potentials to spread rapidly in introduced habitats in the future (Drenovsky et al., 2012). Animals that depend on these native plants for food or shelter are also disrupted because the variety of the native habitat is reduced. Therefore, their spread has led to the disruption of ecosystems stability and overall economic productivities of areas invaded (Dickie et al., 2014; Foxcroft et al., 2017; Hulme et al., 2013). Beside these alien plants, many naturalized plant species have become widely spread, negatively affected the biodiversity of the areas concerned and thereby turned to be invasive (Essl et al., 2019; Lambertini et al., 2011; Simberloff et al., 2013). Many regions of the world have been reported to have varying types of naturalized plant species (Pysek et al., 2017).

Plants invasions are regarded as global issues that negatively influence biodiversity and ecosystem function (Jeschke et al., 2014; Lugo, 2004; Mooney and Hobbs, 2000; Tokhtar, 2018), most importantly when they occupy already disturbed ecosystems (Mostert et al., 2017; Richardson et al., 2014; Rundel et al., 2014). They are naturally stimulated, but can also be triggered by various anthropogenic activities such as land clearing, waste disposal, animal grazing and human movements (Mack, 2005). They are considered as the second most important agents responsible for biodiversity loss and extinction (Blackburn et al., 2004; Lisetskii et al., 2016). The impacts of plant invaders and the corresponding costs of researches on their ecology, management, and control have been predicted to increase across the globe (Sorte, 2014). Plant invaders reduce richness and abundance of native species by preventing the seedling establishment, inhibiting growth and development, modifying plant-pollinator interactions, increasing above and below-ground competition and swamping native gene pools *via* interbreeding with native species of the environment (Ellstrand and Schierenbeck, 2000; Schei, 1996).

The extent of the impact of plant invaders has been linked to their abundance in such communities invaded (Kumschick et al., 2014; Le Maitre et al., 2016). This means that the higher their abundance or biomass in the communities, the higher the impacts (Kotze et al., 2019). Invasive plants also affect ecological processes and physical resources of the ecosystem such as nutrient cycling, sedimentation and disturbance regimes (Mack et al., 2000; Vilà and Hulme, 2017) and eventually restrain ecosystem services, which are fundamental to well-being and survival of humans (Pejchar and Mooney, 2009). Researches on plant invasions so far have been plants community-based and the subsequent effects on the structure and productivity of an ecosystem, changes in biodiversity and other ecosystem-related factors (Mooney and Hobbs, 2000; Sutherst, 2000). As reported by invasive species specialist group (ISSG), there are about 100 world's worst invaders that were classified based on the intensity of their effects on biodiversity and their ability to satisfy certain conditions concerning biological invasion (Lowe et al., 2000; Luque et al., 2014; Richardson and Rejmánek, 2011). Borokoni and Babalola (2012) reported 487 protected areas in 106 countries with invasive species recorded as threats.

The report covers Asia, Africa, South and Central America (including Mexico and the Caribbean) and Europe. In economic terms, invasive species have been estimated globally to cost USD 400 million annually because of revenue loss and costs of control measures. At the same time, about USD 60 million is spent annually on their control in Africa. Almost all countries in Africa have been affected by invasive plant species. The IUCN–World Conservation Union identified 81 invasive plant species in South Africa, 44 in Swaziland, 28 in Egypt, 37 in Algeria and Madagascar, 49 in Mauritius, 22 in Ethiopia, 35 in Kenya and 26 in Ghana and Zimbabwe (Baillie et al., 2004). However, very little is known about invasive alien species (IAS) in Nigeria (Borokini, 2011).

Some researchers have proposed several hypotheses concerning the geographical spread pattern of invasive plants across the world. Some hypothesized that island regions of the world are more likely to be invaded than the mainland (Dawson et al., 2017; Moser et al., 2018; Van Kleunen et al., 2015), southern hemisphere areas are more prone to plant invasion than northern (Richardson and Pyšek, 2012), the massive migration of Europeans in New World regions made them more invaded by plants than Old World regions (Van Kleunen et al., 2015), current and history of human impacts on the environment determines the differences in the extent of invasions among regions of the world (Essl et al., 2011), and the richness of the naturalized plants is more enhanced by socioeconomic factors than invasive plants richness (Williamson, 2006). Despite all these hypotheses, there is still a paucity of comprehensive researches on the drivers of invasive and naturalized plants globally (Essl et al., 2019).

A very vital issue in managing and controlling invasive alien plants (IAP) is having adequate information on their size, density, and distribution. Although IAP species and biological invasions have been widely researched, there are still many insufficient data on the accurate IAP spatial distribution (Chytrý et al., 2009). Satellite remote sensing has been a relevant technique in the early detection of invasions, mapping invasive plant species and development of management strategies for controlling invasions. For proper policy decision making, there is a need for objectivity in IAP distribution data (McNaught, 2005). Also, the application of remote sensing techniques has made it possible to have accurate species observation, and removal of specific plant populations.

There has been the successful mapping of the distribution of a lot of plants together with their ecosystems, and other environmental factors enhancing invasions such as bio-climatic conditions using integrated geographical information system (GIS) and satellite remote sensing techniques (Haltuch et al., 2000; Los et al., 2002; Stow et al., 2000). GIS-based species (niche) modelling techniques have been widely used to analyze species distributions because they are able to infer the relationship between environmental factors and distribution of species through using limited available data on the species occurrence (Guisan et al., 2002; Weiers et al., 2004). It is mostly impossible to get reliable data on the absence of species in habitat due to a lot of limitations in field samplings including inadequate sampling, time constraints, and high cost of surveys. Therefore, reliable species models prefer to make use of presence data only (Anderson et al., 2003).

Ferns (Pteridophytes) which have spread across diverse areas of the world have their origins in the ancient tropical regions (Umi Kalsom, 2010). They are mostly referred to as vascular cryptogams, which mean they possess hidden reproductive organs and some elements of vascular bundles for adequate conduction of water and food materials (Umi Kalsom, 2010). These ferns are an essential component of natural flora and biodiversity of many parts of the world and as such can be regarded as contributing significantly to ecosystem processes (Haque et al., 2016). Despite their widespread in many tropical and sub-tropical regions of the world, they are still being threatened into extinction by a lot of climatic and edaphic factors (Dixit, 2000). These threats, coupled with some natural processes, have been able to transform some ferns to become strange invaders of many different types of environments.

Fern invasions, including their impacts on immediate environments, have not been adequately studied by ecologists globally (Haque et al., 2016). Although extensive researches have been focused on their taxonomy, evolution, and economic importance, yet their ecological studies are mostly ignored (Watkins Jr, 2011). Researchers have focused more on the invasion ecology of higher plants (angiosperms) in many nations of the world. Ferns are known to have the potentials for invading soils with less amount of nitrogen and calcium (i.e. nutrient-deficient soils) and consequently make the soils more fertile (Mehltreter et al., 2010). These invasive ferns have the extraordinary ability to tolerate environmental abiotic stresses, and they are involved in the ecological restoration of disturbed soils (Watkins Jr, 2011).

Pneumatopteris afra (Christ) Holttum **(**Plate 1.1**)** belongs to the family Thelypteridaceae (Agnew, 1974) of the Order Polypodiales, Class Polypodiopsida, and the Division Pteridophyta (Roux, 2009). Thelypteridaceae belongs to the polypodioid ferns with about 1000 species distributed worldwide with a centre of diversity in the Old-world tropics. These plants usually grow in forests, swamps, or near streams (Holttum, 1982; Schelpe and Anthony, 1986) and exhibit extensive morphological diversity. *Pneumatopteris afra* which is also identified as *Cyclosorus afer* (Christ) Ching. has widespread in some African countries including Gabon (Mundy, 2000); Equatorial Guinea (Velayos et al., 2013); Ghana, Cameroon, Sierra Leone and Liberia (Mazumdar, 2013) and Togo (Abotsi et al., 2018). This plant was reported to have been introduced to Nigeria in the early 1960s for aesthetic purposes. It was observed that the fern has the potentials to rapidly grow and colonize wetlands in Nigeria because it could adapt to varying soil conditions and colonize bare land readily (Oloyede et al., 2011). Other reports stated that the fern has extensive colonization and distribution in many wetlands in South Western (Awodoyin et al., 2013) and North Central Nigeria (Akomolafe et al., 2017; Akomolafe and Sulaimon, 2018).

Pneumatopteris afra occurs mostly in marshy to waterlogged habitats in the Southwestern rainfall belt of Nigeria (Oloyede and Odu, 2011). New fronds with the compound leaf formation are usually established by the unfolding of crosiers (Plate 1.2). The arrangement of the sori is on the lower (abaxial) surface of the leaflets.

Each sorus houses a lot of sporangia which are covered with indusia (Alston, 1959). Inside each sporangium lays a mass of small-sized light numerous spores. The continuity and distribution of this plant are enhanced by the spore production and dispersal. Suitable environment, adequate nutrients, unhindered spore dispersal and protection are needed for the spore germination. It also possesses high aesthetic values and spreads rapidly (Oloyede et al., 2011). The fern has rapid growth and observed to be overpopulating most wetlands in some parts of Nigeria. This could have been supported by the unusual invasion promoting features of wetlands which include being regularly disturbed, enough water supply and reserved nutrients (Zedler and Kercher, 2004). However, this large biomass creates severe problems due to water loss by evapotranspiration, the mechanical obstruction of irrigation and drainage canals and can cause changes which affect other organisms.

Plate 1.1 Fronds of *P. afra* on the field

Plate 1.2 Picture of *P. afra* showing the unfolding of the crozier.

1.2 Statement of Research Problem

Pneumatopteris afra is growing abundantly in most wetlands in some parts of Nasarawa State, North Central Nigeria (Akomolafe et al., 2017). The species often dominate these wetland communities by forming large monospecific colonies. Its colonization of these wetlands has caused a physical barrier to the flow of water and threatened the survival of aquatic fauna and flora (Akomolafe and Rahmad, 2018). A lot of native dwellers who depend on the water from these wetlands for farming and other domestic activities must devise alternative means of water supply due to the obstruction of water flow by this fern. This invariably could have affected the economic productivities of the immediate environments colonized by *P. afra*. Despite its recent colonization of wetlands, there is still insufficient information on its habitat requirements which could assist concerned government agencies to properly plan for the restoration and management of those invaded wetlands.

Therefore, understanding the underlying mechanisms that enable it to become invasive is thus necessary before adequate control measures can be implemented (Padalia et al., 2014). This could be achieved by predicting the environmental factors promoting its colonization in Nigeria. As reported by Sakai et al. (2001), investigating the physiological, ecological, and morphological attributes of an invader could enhance a better systematic understanding of the likely mechanisms underlining its invasion success. Also, there are a lot of research gaps in the soil factors requirements of this fern in the invaded wetlands. Therefore, it is vital to examine and compare the soil parameters of invaded and non-invaded wetlands with a view to isolating soil factors that mostly influence the plant abundance, diversity, and richness of those wetlands.

1.3 Justification

The fundamental aim of every invasion ecological studies is to understand the drivers/mechanisms of invasion successes of plants in various ecosystems (Murphy, 2019). Apart from the field observations of the occurrence of *P. afra* and its colonization of wetlands in Nigeria, researchers have not focused on its ecology and likely abiotic factors enhancing its colonization success. This has led to a paucity of its ecological and physiological data. Research priorities are focused on identifying, controlling, and ideally eradicate invasive species. Control and eradication of invasive species are however challenging, costly and often impracticable when an invasion has already progressed too far. Hence, early detection and reliable prediction of areas at risk of invasion are of primary concern (Garner et al., 2019). Also, effective management programs for invasive plant species must be based on adequate knowledge of the target species' biology and ecology. Developing reliable predictive models of future invasions requires a mechanistic understanding of the species and community dynamics which allow an invasive species to invade and establish itself in a new area, as well as a robust quantification of the invasive potential of the plant. This study can then be regarded as the first detection of the invasive potential of *P. afra* in Nigeria.

1.4 Research Aim and Objectives

This research aims to use spatial predictive modelling, ecological and functional trait approach to obtain a mechanistic understanding of the community dynamics and ecosystem properties of *P. afra* invaded and non-invaded wetland communities in some parts of Nigeria.

The specific objectives of this research are:

i. To map the distribution of *P. afra* with environmental variables and develop a dynamic species distribution model in predicting areas of future invasions of *P. afra* in Lafia and entire Nigeria.

ii. To evaluate the impacts of invasions of *P. afra* on plant diversity and richness of residents invaded wetland communities in Lafia, Nigeria.

iii. To evaluate the community characteristics of non-invaded wetlands and compare with those of invaded ones in Lafia, Nigeria.

iv. To assess the functional traits distribution and physiological characteristics of *P. afra* in established, monospecific stands at those invaded wetlands.

v. To determine the soil factors that promote the abundance of *P. afra* at the invaded wetlands, and to also compare the soil parameters of both invaded and non-invaded wetlands in Lafia, Nigeria.

1.5 Research Questions

Based on the research gaps and objectives, the following research questions were answered:

i. What are the bioclimatic variables that predict the habitat suitability of *P. afra* in Lafia and entire Nigeria? Also, what are the future areas and probability of distribution of *P. afra* in Lafia and entire Nigeria?
ii. Does the abundance of *P. afra* at those invaded wetlands have any impact on the resident plant diversity?
iii. Are there any similarities or differences in the diversity indices between the invaded and non-invaded wetlands?
iv. What are the functional traits exhibited by *P. afra* that could be determinants of its assemblage at those invaded wetlands? Are these functional traits limited to any of the invaded sites or common to all the invaded sites?
v. Are there any differences or similarities in soil factors between the invaded and non-invaded wetlands? Do the soil factors influence the colonization of *P. afra* and plant diversity of the invaded wetlands?

1.6 Outline of the Thesis

This thesis comprises eight chapters which can be categorized into five main research chapters (chapters 3-7) and three general chapters (chapters 1, 2 and 8). Each main research chapter represents each specific study objective where the methodology, results and discussions are presented in details (Figure 1.1). However, the general chapters are made of the Introduction (chapter 1) where the general background of the study is given; Literature review (chapter 2) where the study key topics were discussed systematically with reference to past and recent similar studies; and General discussion, conclusion and recommendation (chapter 8) where a general overview of the entire study chapters together with conclusive remarks and some recommendations for future research was presented.

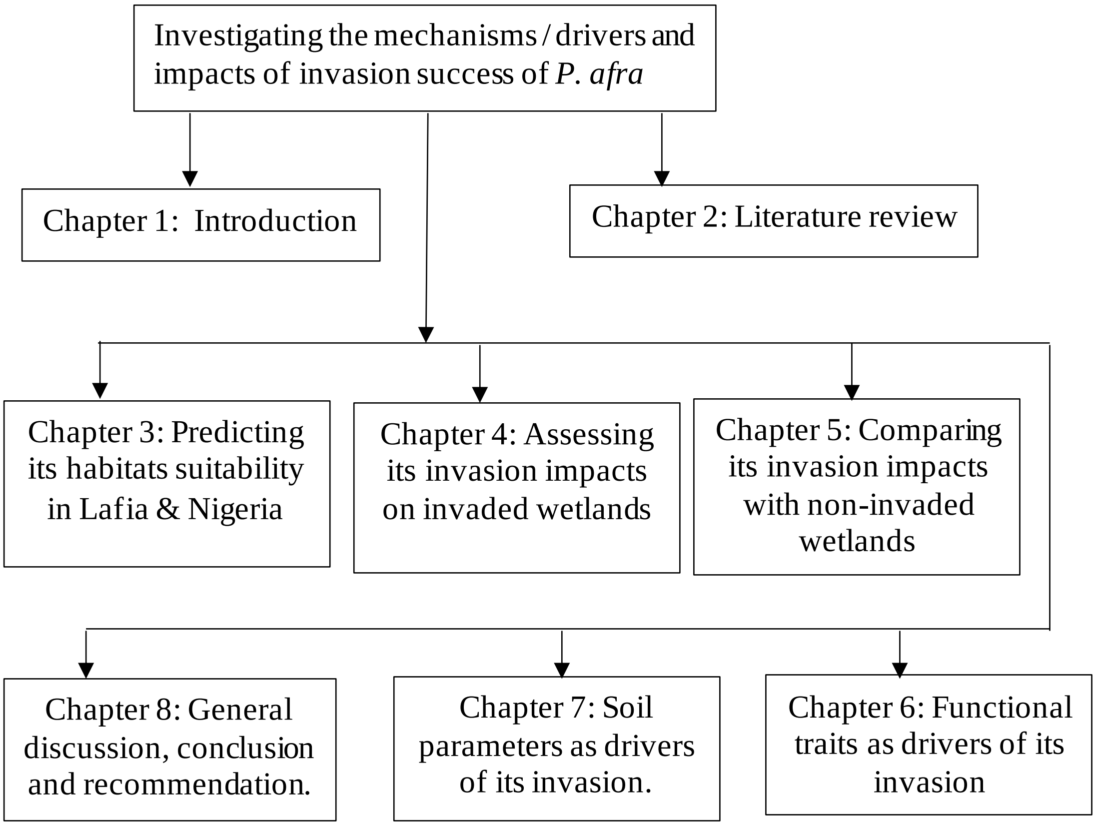

Figure 1.1: A Flow chart showing the arrangement of the thesis chapters

CHAPTER 2

LITERATURE REVIEW

2.1 Description of Some Invasive Ferns

Here are some of the ferns reported to be invasive across the world. These ferns have been highlighted and arranged based on the continents invaded (Table 2.1).

Table 2.1 Checklist of some invasive ferns in different continents

Continent	Country	Invasive Ferns	Source
Africa	Cameroon	*Pityrogramma calomelanos*	Wardlaw (1962)
	Nigeria	*Cyclosorus afer*	Akomolafe et al. (2017)
	South Africa	*Azolla filiculoides*	McConnachie et al. (2003)
Asia	Malaysia	*Acrostichum spp.*	Jawa and Srivastava (1989)
	Iran	*Azolla filiculoides*	Sadeghi et al. (2012)
Australia	Australia	*Pteridium aquilinum*	
	New Zealand	*Pteridium aquilinum*	Marrs et al. (2000)
Europe	Britain	*Pteridium aquilinum*	Marrs and Watt (2006)
	Poland	*Azolla filiculloides*	Myśliwy and Szlauer-Łukaszewska (2017)
	Italy	*Salvinia molesta*	Giardini (2004)
North America	Mexico	*Pteridium aquilinum*	Schneider and Fernando (2010)
	USA	*Pteridium aquilinum*; *Lygodium microphyllum; Lygodium japonicum; Pteridium arachnoideum*; *Azolla pinnata; Dennstaedtia punctilobula; Thelypteris noveboracensis*, *Asplenium adiantum-nigrum; Dryopteris carthusiana; Dryopteris intermedia; Polystichum acrostichoides*	Flinn (2006); Hill (1996); Madeira et al. (2013); Ranker (2016); Volin et al. (2004)
	Canada	*Pteridium aquilinum*	Schneider (2006)
	Costa Rica	*Angiopteris evecta*	Christenhusz and Toivonen (2008)

	Jamaica	*Angiopteris evecta*	Christenhusz and Toivonen (2008)
South America	Brazil	*Pteridium arachnoideum*	Miatto et al. (2011)

(i) *Angiopteris evecta* (Forst.) Hoffm

Angiopteris evecta (oriental vessel fern) which originated from South Pacific, has been reported to have invaded several countries in North America such as Costa Rica, Jamaica, and Hawaii. In these countries, this plant was able to colonize new territories and alters native biodiversity effortlessly (Christenhusz and Toivonen, 2008).

(ii) *Azolla filiculoides* Lam.

Azolla filiculoides (Redwater fern) is an aquatic fern that is native to South America. It has been found to have occupied wetlands in Iran, South Africa and other countries in Africa and southeast Asia (Hashemloian and Azimi, 2009; McConnachie et al., 2003; Sweet and Hills, 1971). This fern has a fast-growing ability within five days, and this makes it a unique invader of aquatic communities (Taghi-Ganji et al., 2005; Van Hove and Lejeune, 2002). It is also able to establish a mutualistic relationship with some bacteria, thereby fixing nitrogen (Fernández-Zamudio et al., 2010). Its invasion has been linked with the eutrophication of aquatic communities (Barreto et al., 2000). It has caused lots of economic hardships to the inhabitants of areas concerned by obstructing water flow and limiting the amount of water needed for use.

(iii) *Dennstaedtia punctilobula* (Michx.) T. Moore

Dennstaedtia punctilobula (Hayscented fern), is a fern that is native to Canada and the USA. It has adversely affected the regeneration and survival of forest plants in most forests in the USA and North America (Hill, 1996). This, coupled with its rapid colonization, made it regarded as one of the world's aggressive invaders (Hill and Silander Jr, 2001). It was also observed invading some roadsides and forests in New England (Hammen, 1993).

(iv) *Dryopteris intermedia* (Muhl.) Gray and *Dryopteris carthusiana* (Villars) Fuchs

These invasive ferns belonging to the same genus were problematic in hilly forests in North America and the USA (Singleton et al., 2001). They became successful there as a result of the long-distance dispersal of their spores by the wind. Although they have a similar mode of spread, they still occupied different geographical territories in the USA (Flinn, 2006).

(v) *Lygodium microphyllum* (Cav.) R.Br.

Lygodium microphyllum (old world climbing fern) has been found to have occupied a large portion of pinelands, swamps, and islands in South Central Florida (Kurumatani et al., 2001). It is described by its ability to cover other plants using its strong and thick vines. *Lygodium microphyllum* also alters some ecosystem processes in areas invaded. Therefore, by disallowing these understory plants from accessing adequate sunlight, they become entirely removed from the forests. This fern has a complex mode of reproduction, including intra and inter-gametophytic selfing with a high spore germination rate. Also, the fern was able to rapidly invade these habitats due to its faster rate of completion of its reproductive cycle (alternation of generation) (Lott et al., 2003).

(vi) *Pityrogramma calomelanos* L.

Pityrogramma calomelanos was described as a stubborn invader of oil palm plantations in Cameroon (Africa). The history of its invasion was traced to the period when arsenical herbicide was applied on a leguminous weed called *Pueraria phaseoloides* which was affecting oil palm plantations. This gave room for the fern to overpopulate the entire farms. *Pityrogramma calomelanos* has adaptive features for surviving extended dry period, but only reproduce sexually during the wet season (Wardlaw, 1962).

(vii) *Polystichum acrostichoides* (Michaux) Schott

Polystichum acrostichoides (Christmas fern) which is a native of North America, has been a stubborn invasive evergreen fern in many primary forests in New York, USA. It is a perennial fern that occupies diverse habitats such as forest shades, slopes, woodlands, and banks of streams (Flinn, 2006).

(viii) *Pteridium aquilinum* (L.) Kuhn

Pteridium aquilinum **(**Bracken Fern), has been successfully established as an invader of most parts of the world except in places with extremely high temperatures and less moisture. This fern originated from Britain (Marrs and Watt, 2006; Taylor, 1990). It has restricted the regeneration of forest trees and caused significant loss of viable agricultural land, thereby leading to the economic breakdown of areas invaded. As a result of the aggressive underground rhizome, the control of *Pteridium aquilinum* has been challenging to achieve. Therefore, it was able to take over many habitats both disturbed and undisturbed, thereby posing threats to native biodiversity (Der et al., 2009; Roos et al., 2011). Its means of spore dispersal, whereby it disperses throughout the whole year makes its invasion successful in most tropical countries (Schneider, 2004). Besides this, *P. aquilinum* is allelopathic by preventing the growth of nearby plants and possess chemicals for fighting attacks from disease-causing organisms (Alonso-Amelot and Avendano, 2002; Marrs et al., 2000). This fern can also be described as having phenotypic plasticity, which enables it to adapt to different favourable and harsh environments. This makes it outcompete the native plants in the same place (Page, 1986). Its successful invasion in Southern Yucatan for many years has led to a drastic reduction of cultivated land (Schneider, 2006). Frequent fire and clearing of land for agricultural purposes have enhanced its successful invasion in many secondary forests. This fern can conveniently be regarded as invasive due to its difficulty in control and reduction of native biodiversity (Schneider and Fernando, 2010).

(ix) *Pteridium arachnoideum* (Kaulf.) Maxon.

Pteridium arachnoideum (neotropical bracken fern) has been observed to be invasive in the Brazilian Cerrado, South America. In this region, it was able to alter the native vegetation structure by reducing plant diversity and density, which makes it a threat (Miatto et al., 2011).

(x) *Salvinia molesta* D.S. Mitchell

Salvinia molesta, a noxious invasive fern that originated from Brazil is problematic in Italy. Also, this fern has widespread in many tropical countries. *Salvinia molesta* can grow extensively over surfaces of water bodies within a very short period (Giardini, 2004).

(xi) *Sphaeropteris cooperi* (W.J. Hooker ex. Mueller) Tryon

The invasion of *Sphaeropteris cooperi* (Australian tree fern) in some forests in Hawaiian (North America) has successfully led to the complete removal of many native plant species including ferns. This fern is an evergreen one that is known for its fast-growing nature. This makes it spread faster and occupies new territories that native plants could not (Chau et al., 2013).

(xii) *Thelypteris noveboracensis* (L.) Nieuwl

Thelypteris noveboracensis (New York fern) has also been reported to be invasive in the USA due to its ability to interfere with forest regeneration (Hill and Silander Jr, 2001). This fern usually grows abundantly, thereby inhabiting the understory of some regrowth forests in Connecticut, USA.

2.2 Species Distribution Modelling

2.2.1 What is Species Distribution Modelling?

Species distribution models (SDMs) which are also known as ecological niche models (ENMs) are mathematical tools that quantify the relationship between species occurrence and distribution in a location and the environmental variables or factors of the same location where it has been found (Guisan and Zimmermann, 2000; Hageer et al., 2017; Yang et al., 2013). They are also regarded as ecological niche models (Elith and Leathwick, 2009) used for predicting and understanding biodiversity spatial forms (Pradervand et al., 2014) through the use of maps of the environmental variables acting as predictors (Elith and Franklin, 2013). Several ecological studies have quantified this species distribution - environmental factor relationships many years ago, and they have been able to predict past, present and future distributions of species based on changing environmental factors (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). Besides, SDMs are also used for the management of areas having endangered species (Zhang et al., 2012).

Prediction of distribution and occurrence of plant species is critical in ecological conservation rather mere locating where such species are found (Rushton et al., 2004). SDMs have been extensively utilized in environmental, and biogeographical studies in the past two decades with the development of several novel methods (Elith et al., 2011). Habitat niche modelling as it is also called is a viable tool used in modelling changes in vegetation structure of a place, prediction of future changes, developing proper management plans and assessing invasion risks (Falk and Mellert, 2011; Santamarina et al., 2019). This has been made possible with recent developments in satellite remote sensing and geographical information systems (Mahiny and Turner, 2003). Apart from using SDMs in the autecology of species, they have also been harnessed in assessing the effect of environmental changes and land use on species distributions (Guisan and Theurillat, 2000). It is also used to produce the floras and conservation plans of some areas (Margules and Austin, 1994).

The success of biodiversity conservation in recent years has been attributed to modelling and mapping the distribution of species. The use of traditional ecological floristic surveys in determining species distribution has proved inaccurate in the past, unless when such investigations are focused on single species within a minimal location. This is mainly because of bias in sampling methods and the difficulties in determining the exact ecological points of occurrence of such species (Pallaris, 1998). Also, SDMs could help implement the use of appropriate control and conservation techniques and policies. According to Elith and Leathwick (2009), main steps involved in modelling techniques include assembling significant data; determining its sufficiency (both species occurrence data and environmental predictors); managing highly correlated variables; selecting the best-fitting model; allocating training and test data to the model; model evaluation or assessment of model accuracy; mapping the predictions to a particular geographic location; threshold selection for continuous predictions; model improvement if necessary.

2.2.2 Classification of Species Distribution Models

Researchers have established several categories for classifying distribution models (Franklin, 2010). Firstly, models that are based on predicting the species response within a fundamental reality are known as mathematical or analytical models (Pickett et al., 2010; Sharpe, 1990). Secondly, models based on predicting exact cause-effect relationships that are biologically important to species are regarded as physiological, mechanistic, or causal models (Decoursey, 1992; Prentice, 1986). The third category of models is referred to as phenomenological, statistical, or empirical models because they were not designed to explain species responses and cause-effect relationships, but to gather empirical proofs (Pickett et al., 2010; Sharpe and Rykiel, 1991; Wissel, 1992). In all the models, there are four main standard components which are information on the presence, absence or abundance of a target species; a set of environmental variables which may be quantitative or categorical; the mathematical model which computes the relationships between species occurrence and environmental variables; and validation of the model prediction accuracy (Robinson et al., 2017; Rushton et al., 2004).

The interests of researchers on species distribution models have increased geometrically over the years (Guisan et al., 2014) and this has led to the development of several models in prediction of species distributions (Barbosa et al., 2012; Leidenberger et al., 2015). These models can relate species occurrence data (absence or presence) with relevant environmental variables, and then generate the probability of distributions of such species which are projected over particular study areas (Carlos-Júnior et al., 2015; Mellin et al., 2016). Some of the most widely utilized models include Generalized linear models (GLM), genetic algorithm for rule-set production (GARP), bioclimatic (BIOCLIM) and maximum entropy (MAXENT). The availability of presence and absence data of target species are usually employed in multi-purpose distribution models whereas some specific models are based on presence data only (Phillips et al., 2006). Examples of such multifunctional models that are less frequently used by ecologists because of the paucity of absence records include Support Network Machines (Pouteau et al., 2011; Sadeghi et al., 2012) and Artificial Neural Networks (Kulhanek et al., 2011). All SDMs do complement each other (Elith and Graham, 2009). Thus, it is advisable to test different models for predicting a species distribution (Castelar et al., 2015; Farashi and Najafabadi, 2015). However, the choice of a model still depends on availability and number of presence/absence data, size of predicted geographical area and nature of environmental variables that relate with species ecology (Padalia et al., 2014).

(a) Generalized Linear Models (GLM)

The generalized linear model is described as a mathematical equation that contains mathematical, parameters, and random variables that are linear. Logistic regression models have been more commonly used in modelling species distribution because a single species occurrence record (whether presence or absence) of a specific species can be considered to be a binomial trial using a minimum sample size of 1 (Rushton et al., 2004). The two main assumptions in any GLM techniques are that the predictor variables are sufficient in determining the distribution pattern of the species and the error structure is suitable for the data (Rushton et al., 2004). An alternative form of GLM called Generalized Additive Models (GAM) has also been used extensively for predicting species distribution (Elith et al., 2006; Guisan et al., 2006).

(b) Maximum Entropy (MAXENT)

Maximum Entropy (Maxent) is a machine learning, highly competitive and recently developed species distribution model which is the most widely employed in predicting the current and future distribution of species across local, regional and global scales (Coro et al., 2015; Fois et al., 2018; Morales et al., 2017; Phillips and Dudík, 2008; Phillips et al., 2004; West et al., 2016). Non-governmental and Governmental organizations have used Maxent for several biodiversity mapping projects (Elith et al., 2011; Hernández-Quiroz et al., 2018; Koch et al., 2017; Lamsal et al., 2018; Morales, 2012). Maxent operates with the principle of approximating the probability distribution of species based on maximum entropy by making predictions from inadequate or incomplete data (Phillips et al., 2006).

Maxent is a model that is based on presence data only (Ficetola et al., 2007) and it is known to perform better than other model types (Farashi and Alizadeh-Noughani, 2018). Presence only data has solved the challenge of unreliable absence data (Jiménez-Valverde et al., 2008). This is also because it is difficult to accurately get absence data of species when conducting field surveys as a result of limiting factors such as resources and time. There may also be situations whereby false absence data are recorded on the field, thereby affecting the reliability of distribution models (Elith et al., 2011). The models that operate based on presence data only are regarded as highly valuable (Graham et al., 2004). Maxent model is very biased sensitive. Therefore, accuracy should be ensured in obtaining the presence data to improve the model performance (Elith and Leathwick, 2009).

(c) Artificial Neural Networks (ANNs)

These are the machine-learning models rarely used in ecological modelling (Gevrey et al., 2003; Olden et al., 2004). They usually model between input and output vectors of real numbers which do produce non-linear functions (Coro et al., 2018). A learning algorithm can be used to train an ANN model type to produce function based on already known data. After this, the result of the trained ANN can then be tested using other known data as test data. This is achieved by running the model several times to avoid errors (Özesmi et al., 2006). One main disadvantage with the use of ANNs is that they usually fail to produce the analytical form of the produced function and it is complicated to understand how the input data are integrated inside the network (Coro et al., 2018).

(d) Support Vector Machines (SVMs)

The support vector machine is also another type of machine learning model, which is used in species distribution modelling (Brown et al., 1999; Guo et al., 2005). It is popularly used for classifying various categories of remotely sensed data including hyperspectral, multisensor and optical data (Foody and Mathur, 2006; Lennon et al., 2002; Waske and Benediktsson, 2007). Its use has gained widespread among researchers because it could be applied to different fields of studies (Hoang et al., 2010; Keerthi et al., 2001; Zarkami et al., 2012). It works based on the principle of using a Kernel function to project input data to a simpler but high dimensional space (Vapnik, 2013). This model can maximize the distance between the support vectors using a hyperplane (Coro et al., 2018). Support vector machines have also been used for selecting input variables whose quantity of information is the highest (Chang, 2011; Vilas et al., 2014). It has been designed to work with complex and non-linear data (Akkermans et al., 2005; Sadeghi et al., 2012). By default, this model can replace missing values and transform nominal data into binary (Witten et al., 2016).

(e) Genetic Algorithm for Rule-Set Production (GARP)

The genetic algorithm for rule-set production is another type of machine learning modelling technique used for predicting species distributions based on genetic algorithm (Stockwell, 1999). It has also been used to predict species distribution with presence-only data accurately (Hijmans and Graham, 2006; Phillips and Dudík, 2008). GARP works by randomly creating sets of mathematical rules which produce the potential species niche influenced by environmental variables (Padalia et al., 2014). These mathematical rules are usually produced following the default process of selection, testing, and integration or rejection (Peterson et al., 2007). Studies based on forecasting potential risks of sites susceptible to invasion by matching the environmental requirements of species at their native and introduced ranges have been successfully achieved using GARP (Ganeshaiah et al., 2003; Underwood et al., 2004).

2.2.3 Environmental Predictors of Species Distributions

The environmental factors that determine the geographical distribution of species in certain habitats are known as predictors, covariates, or independent variables in species distribution models (Elith et al., 2011). Species distributions are determined by distinct sets of eco-physiological and other factors such as anthropogenic disturbances, dispersal means, and biotic interactions which could be positive or negative (Soberón, 2007). It should be noted that these predictors of species distributions do not act in isolation but do influence each other in determining the occurrence of a plant species (Agrawal et al., 2007; Michalet et al., 2006). In selecting environmental variables to be used in SDMs, the quality and significance of such variables to the ecology of species concerned are to be considered (Austin, 2007; Austin and Van Niel, 2011; Fourcade et al., 2014) in order to avoid some errors