Assessing the impact of invasive plants in the Northern Western Ghats and surrounding savannas

विद्या वाचस्पति की
उपाधि की अपेक्षाओं की आंशिक पूर्ति में प्रस्तुत शोध प्रबंध

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द्वारा / By
मेघा ओझा / Megha Ojha

२०१९३६४७ / 20193647

डॉ. दीपक बरूआ / Dr. Deepak Barua

भारतीय विज्ञान शिक्षा एवं अनुसंधान संस्थान पुणे
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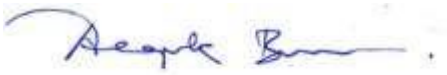
CERTIFICATE

Certified that the work incorporated in the thesis entitled “Assessing the impact of invasive plants in the Northern-Western Ghats and surrounding savannas”. Submitted by Megha Ojha was carried out by the candidate, under my supervision. The work presented here or any part of it has not been included in any other thesis submitted previously for the award of any degree or diploma from any other University or institution.



Dr. Deepak Barua

Supervisor

Date: 29 July 2023

Declaration by Student

Name of Student: Megha Ojha

Reg. No.: 20193647
Thesis Supervisor(s): Dr. Deepak Barua

Department: Biology
Date of joining program: 1 August 2019

Date of Pre-Synopsis Seminar: 3 May 2024

Title of Thesis: Assessing the impact of invasive plants in the Northern-Western Ghats and surrounding savannas

I declare that this written submission represents my idea in my own words and where others' ideas have been included; I have adequately cited and referenced the original sources. I declare that I have acknowledged collaborative work and discussions wherever such work has been included. I also declare that I have adhered to all principles of academic honesty and integrity and have not misrepresented or fabricated or falsified any idea/data/fact/source in my submission. I understand that violation of the above will be cause for disciplinary action by the Institute and can also evoke penal action from the sources which have thus not been properly cited or from whom proper permission has not been taken when needed.

The work reported in this thesis is the original work done by me under the guidance of

Dr. Deepak Barua
Date: 29 July 2024
Signature of the student 

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"What we observe is not nature in itself, but nature exposed to our method of questioning."

Werner Heisenberg

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Contributions

Chapter	Contribution	People involved
Chapter 1	Writing	Megha Ojha
Chapter 2	Conceptualisation	Megha Ojha, Deepak Barua
	Data collection	Megha Ojha, Mandar Datar, Prerna Agrawal, Ashish Nerlekar, Bhanudas Chavan
	Analysis	Megha Ojha, Deepak Barua, Ovee Thorat
	Writing - Initial draft	Megha Ojha
	Writing - Feedback	Deepak Barua
	Supervision	Deepak Barua
Chapter 3	Conceptualisation	Megha Ojha, Deepak Barua
	Data collection	Megha Ojha, Akanksha Ingale, Bhanudas Chavan
	Analysis	Megha Ojha, Akanksha Ingale, Deepak Barua
	Writing - Initial draft	Megha Ojha
	Writing - Feedback	Deepak Barua
	Supervision	Deepak Barua
Chapter 4	Conceptualisation	Megha Ojha, Deepak Barua
	Data collection	Megha Ojha, Bhushan Shigwan, Ashish Nerlekar, Bhanudas chavan, Mandar Datar, Deepak Barua
	Analysis	Megha Ojha, Deepak Barua, Ashish Nerlekar
	Writing	Megha Ojha, Deepak Barua, Ashish Nerlekar
	Funding acquisition	Megha Ojha (ATBC seed grant)
	Supervision	Deepak Barua
Chapter 5	Conceptualisation	Megha Ojha, Deepak Barua
	Data collection	Megha Ojha, Bhushan Shigwan, Ashish Nerlekar, Bhanudas chavan, Mandar Datar, Deepak Barua
	Analysis	Megha Ojha, Deepak Barua
	Writing	Megha Ojha, Deepak Barua
	Funding acquisition	Megha Ojha (Trimurthi fabricators)
	Supervision	Deepak Barua
Chapter 6	Writing	Megha Ojha

SYNOPSIS

Title: Assessing the impact of invasive plants in the Northern-Western Ghats and surrounding savannas

Name: Megha Ojha

Registration number: 20193647

Name of Supervisor: Dr. Deepak Barua

Department: Biology

Date of registration: July 31, 2019

Indian Institute of Science Education and Research (IISER) Pune

Chapter 1: Introduction

Invasion by non-native species is one of the leading causes of global biodiversity loss and species extinction. There has been a rapid increase in number of non-native species across the globe and this is expected to increase in the future. Invasive plants negatively impact biodiversity at different levels of organization. They cause reduction is population sizes, and change composition of native communities in an ecosystem. Such changes in community structure/composition can further impact the ecosystem functions and services. Since the 15th century AD, invasive species have contributed to 60% of the total global species extinctions. Although, the negative impact of invasion has been well established there exists a huge knowledge gap in our understanding of invasive species from the tropical regions. As with any other tropical regions, invasive species are a major cause for concern in the Western Ghats and Konkan regions in peninsular India. However, information on invasive plants from this region is limited. This thesis uses various complimentary approaches for identification, impact assessment and prioritization of invasive plant species from the northern parts of Western Ghats and Konkan region.

Chapter 2: Identifying, characterizing and prioritizing invasive plants of the Northern Western Ghats and Konkan regions

There are several factors that determine successful invasion of a species. These factors can be broadly categorized into two major dimensions: demographic dimensions (Range size, local abundance etc) and impact dimensions (per capita impact). In this Chapter, I identify invasive plants

of NWGK, and use complimentary approaches to quantify their success of along various dimension of invasiveness. Herbaria based approach was used to determine range sizes and temporal dynamics of these species. I used expert based approach to quantify other dimensions such as local abundance and impact of these species in this region. Finally, I used information across these dimensions to identify high priority invasive plants. Invasive plants of NWGK showed differences in their relative ranking along the different dimensions of invasiveness. These species showed considerable variation in their range sizes. Over thirty percent of these species had moderate to high local abundance and half of them showed large habitat breadth. Finally, using expert based approach, six high priority invasive species of NWGK were identified.

Chapter 3: Functional trait distributions and ecological strategies of invasive plants of the Northern Western Ghats and Konkan regions

Plants use different strategies to grow, survive and reproduce in a given environment. The variability in these strategies generated due to variation in environmental conditions or biotic interactions are captured by the functional traits of species. According to the law of limiting similarity, a non-native species will become successful if it has different trait combination from the co-occurring native species. Additionally, invaders are known to have traits associated with higher competition and faster resource acquisition. In this Chapter, trait based approach and CSR ecological strategies were used to study invasive plants of NWGK. The traits related to competition, resource use and reproduction were quantified and their association with different dimensions of invasiveness was established. Additionally, I estimated the difference in the traits of invasive species with co-occurring native savannas species. Invasive species with high resource acquisitive and ruderal strategies had larger range size in this region. They differed from the co-occurring native species in traits associated with competition, corroborating with the law of limiting similarity.

Chapter 4: Differential impact of invasion on plant communities of two functional types of savannas in India

Invasive plants can alter savanna communities in complex ways, and impacts can vary with the intensity of invasion and the spatial scales examined, and are likely modulated by climate. However, our understanding of such impacts on Asian tropical savannas is limited. In this chapter, I assessed

the impact of invasion across a gradient on alpha and beta diversity in wetter broad leaf savanna (BLS) and drier fine-leaf savanna (FLS). I found that species richness and diversity declines linearly with increasing invasion in both savannas. The species loss was higher in BLS than in FLS. At larger spatial scale, there was an increase in beta diversity in BLS whereas no change was observed in the FLS. The observed dissimilarity at larger spatial scale was a function of species turnover. These results reinforce the need to examine the impact of invasion at multiple spatial scales.

Chapter 5: Shift in functional and phylogenetic composition of plant communities across invasion gradient in savannas

Invasion can alter the functional and phylogenetic composition of an ecosystem. Such changes in functional structure of community can impact the ecosystem level functions and services. They also provide insights into the mechanism of invasion (niche filling versus niche expansion). It is therefore critical to estimate the impact of invasion on functional and phylogenetic composition of savannas. In the final chapter of thesis, I estimated the quantified community weighted traits, functional diversity and phylogenetic diversity of savanna communities across an invasion gradient. The results showed that invaded savanna communities had traits associated with higher competition and faster resource acquisition. Additionally, with increasing invasion savannas became more functionally and phylogenetically diverse. This increase was potentially driven by functionally distinct invader and natives, which led to increase in functional diversity.

Chapter 6: Conclusions

This thesis identifies and characterizes invasive plants from the NWGK. Trait based approach shows that invasive plants with ruderal strategies are more successful in this region. Additionally, through this work impact of invasion on taxonomic, phylogenetic and functional diversity in two types of savannas was quantified. This is the first comprehensive study on invasive plants from Western Ghats and also the first study that has assessed impact of invasion at multiple spatial scales in two types of functional savannas in India. The results obtained from this thesis have direct implications for the management of invasive plants in the region.

CONTENT

Chapter 1: Introduction

General background

Invasion by non-native species is considered to be one of the leading causes of biodiversity loss and species extinction (Vilà et al. 2011) . Non-native species are those which are introduced by humans outside their present or past native distribution (Elton 1958). A subset of these non-native species increase their range and abundance in the introduced range and are known as non-native invasive species (Castri et al. 1990). Invasion impacts biodiversity at multiple levels of organization. It causes reduction is native population sizes, or in some cases even local extinction of species. Since the 15th century AD, non-native invasive species have directly or indirectly contributed to 60% of the total global species extinctions (Bacher et al. 2024). Changes in community structure caused by invasion can further have an effect on ecosystem function and services (Vilà et al. 2011). Along with having impact on biodiversity they are also associated with negative socio-economic impacts. Globally, every year invasion leads to loss of $26.8 billion, India has third highest economic cost (next only to USA and Australia) related to invasion (Bacher et al. 2024).

Knowledge gap

There has been an exponential increase in number of non-native species across the globe and this is expected to increase in the future (Anton 2021). Although, the negative impact of invasion has been well established and international bodies have recognized them as a major problem, there is a big knowledge gap on our understanding of invasive species (Bacher et al. 2024). Tropical biomes have high invasion pressure, and are amongst the least studied biomes around the globe.

Although, India is a hotspot for number of established non-native species, with 2.4% of its flora being of non-native origin (Inderjit et al. 2018) and 72% of the natural areas being invaded (Mungi et al. 2023) but there are comparatively fewer studies on invasive species from the subcontinent. Convention of biodiversity recognized the importance of filling this knowledge gap and during their tenth meeting in Aichi, set out targets to identify all non-native species, their introduction pathways and prioritize them by the year 2022. A few studies from the Indian subcontinent have identified and prioritized invasive species (Pant et al. 2021; Sandilyan 2019; Mungi et al. 2019) but not comprehensively. There exists a knowledge gap in study of invasive species from India and even more in the northern parts of the biodiversity hotspot of Western Ghats.

Impact of invasive species is determined by several demographic such as its range size, local abundance and impact dimensions such as its per capita impact (Parker et al. 1999). Species can have differential impact based on these different dimensions. Information on these dimensions can be obtained through the evidence based approach that is by studying specie in field and/or under greenhouse settings. However, this approach is resource intensive and can become difficult to employ on multiple species at larger spatial scale. Another way of generating this information is by using expert based approach which involves interviewing experts on these different dimensions using a questionnaire (Mungi et al. 2019). Ranks of species across different dimensions can then be used to provide an overall ranking to species across all the different dimensions of invasiveness. This ranked list can also be used to identify high priority invasive species.

Trait based approach to study invasion

Identifying the cause of invasion is crucial both for risk assessment and impact quantification of non-native species (Fletcher et al. 2016). There are several theories in the field of invasion biology regarding possible causes of invasion success, but different theories having different degrees of support (Jeschke and Heger 2018). There is no single hypothesis that explains the success of all invasive species. This lack of generality can be addressed by using trait based approaches to study invasion (Westoby et al. 2002). Trait based approach offers a general framework to understand ecological processes and can be incorporated to understand invasive species (Baker 1965; Pyšek and Richardson 2007). Association of invasion with traits go way back to 1965, when Baker mentioned that weedy species have common set of traits which are associated with their weedy habit (Baker 1965). Over time, multiple trait based studies from across different biomes started to emerge. These helped ecologists in identifying traits which were frequently associated with invasive species (Pyšek and Richardson 2007). Subsequently this field started to gain momentum with more studies comparing not just the trait of invasive species but also comparing them with the trait of co-occurring native species (Kleunen, et al. 2010). Comparison between the trait spaces of invasive species with the co-occurring native species helps in understanding both the establishment and impact of invader in native community (Carboni et al. 2016). Further meta-analysis studies have shown that invasive species have higher values for performance related traits than non-invasive species. These differences are more significant when comparing the invader with natives, than with the non-invasive aliens (Kleunen et al. 2010). This rapidly growing field of trait based approach opens up a path towards a more general understanding of cause and impact of invasion.

Impact of invasion on taxonomic, phylogenetic and functional diversity

Invasive species are known to cause negative impact to biodiversity. The negative impact of invasion on biodiversity is not just restricted to the loss of species but can often cause change in functional compositions (Sodhi et al. 2019). Functional and phylogenetic diversity patterns provide insights both into the mechanism and impact of invasion in a system. The impact of invasion on taxonomic/phylogenetic and functional diversity can be a function of nature of invader and/or native community composition. These impacts are also often modulated by the differences in type and strength of environmental conditions of a system compositions (Sodhi et al. 2019). Additionally, the impact of invasion on a community can be scale dependent and impacts from smaller spatial scales cannot be linearly translated to large spatial scale (Powell et al. 2011). Therefore, along with assessing the impact at smaller spatial scale, it is important to quantify the impact at larger spatial scale. Furthermore, diversity analysis at larger spatial scales can also provide insights into the mechanism of invasion. For instance, beta diversity and its components identifies the underlying mechanism (species turnover versus loss) of community change upon invasion (Baselga 2010). Therefore, for a comprehensive impact assessment of invasion, it is important to understand the impact of invasion at different types of diversity (taxonomic, phylogenetic and functional) at multiple spatial scales (alpha and beta) across different ecosystems (Broad leaf savanna and Fine leaf Savanna).

In my thesis, I fill a major knowledge gap in the Norther Western Ghats and Konkan regions, one of the biodiversity hotspot regions of the world. I have used various complimentary approaches for identification, impact assessment and prioritization on invasive plant species from NWGK. This thesis is the first comprehensive study of invasive plants from this region.

In my second chapter I use complimentary approaches to identify and prioritize major invasive plant species of the Northern- Western Ghats and Konkan regions. I used herbaria based approach to study range size and temporal dynamics of the 78 plants which were identified as invasive in this region. Further I used expert based approach to gain insights into other demographic and impact dimension of these species. Finally, high priority invasive plants were identified across different demographic and impact dimensions.

In the third chapter, I studied functional traits and ecological strategies of the invasive plants and explored its relationship with invasion success. I quantified traits related to competition, resource acquisition and reproductive capability. Furthermore, these traits were used to quantify the CSR ecological strategy for the species. I then measured the association between the traits and ecological strategies (CSR) with range size of species obtained from the first chapter. Finally I compared the trait space of the invasive species with the co-occurring native species in broad leaf savannas, a habitat found on the eastern edge of the Northern Western Ghats.

In the fourth Chapter, I quantified the impact of invasion gradient on taxonomic diversity in two types of savanna. There are two types of savannas found near the eastern edge of the Northern Western Ghats, The mesic Broad leaf savanna (BLS) and drier fine leaf savanna (FLS). Since these savannas differ in their mean annual precipitation, I expected differences in both the type of invader and their relative impact in these savannas. To get a comprehensive understanding of the impact, I estimated the impact of invasion on taxonomic diversity at two different spatial scales. I measured various metric of alpha diversity, compositional changes and beta diversity across invasion gradient in these two savannas.

In my final chapter, I assessed the impact of invasion on functional and phylogenetic diversity of communities across a gradient. To assess the impact on functional diversity, I measured several traits associated with competition, resource acquisition and reproduction. I also assessed the shifts in dominant traits of communities across invasion gradient, by measuring shifts in community weighted traits means across several traits both in univariate and multivariate space.

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Chapter 2: Identifying, characterizing and prioritizing invasive plants of the Northern Western Ghats and Konkan regions

Introduction

Biological invasions which are a leading cause of biodiversity loss (Jeschke et al. 2014) have increased rapidly in the last couple of centuries, and are projected to continue increasing in the future (Seebens et al. 2021). Terrestrial ecosystems are the most negatively impacted (Bacher et al. 2024), and primarily by invasive plants (Bacher et al. 2024). Within terrestrial systems, the tropics are second only to temperate woodlands in the number of invasive species they harbour (Bacher et al. 2024). Given the adverse impacts and costs associated with invasive species, there is an urgent need to identify and prioritize invasive plant species to efficiently manage and reduce their impact (Early et al. 2016). Like in other tropical regions, invasive species are a major cause for concern in the Western Ghats and Konkan regions in peninsular India (Kannan, et al. 2013), which are recognized as biodiversity hotspots (Myers 1988). At the same time, this region has also been identified as a biodiversity darkspot (Ondo et al. 2023), with limited information available on plants, particularly invasive species. In this study, I complemented herbarium and literature based approaches to determine range sizes of invasive plants, with expert surveys to comprehensively assess the impact of invasive species in this ecologically unique and important, but understudied region.

The impact of an invasive species is an integrated function of its range size, local abundance, and per capita effect (Parker et al. 1999). The geographic extent of invasive species varies considerably, and is often directly related to the impact of these species in their new ranges (Carr et al. 1992). Additionally, range size is often correlated with other dimensions of invasiveness,

and therefore, commonly used to assess the impact of invasive species (Fristoe et al. 2021, Gallien et al. 2019). Range sizes can be determined from herbarium collections (Miller et al. 2009), Floras (Antunes and Schamp 2017; Pyšek, 1991), global and regional distribution databases (Pagad et al. 2022), remotely sensed data (Elmer et al. 2021), and long term field studies (Mungi et al. 2023). However, some methods like long term field studies and remote sensing are resource and time intensive and therefore, typically restricted to a smaller numbers of species.

Herbarium collections, occurrence data from Flora (book containing list of plants in an area), publications, and global and regional databases are convenient and readily available sources of information that can be used to determine species distributions (Funk, 2003; Ivanova and Shashkov,2021). Such approaches are widely used to determine range sizes to assess the impact of invasive species (Pyšek, 1991). Additionally, this information can be used to construct invasion curves to determine the temporal dynamics of invasive species (Antunes and Schamp 2017). Invasion curves are useful to understand the major phases associated with the spread of invasive species: a) lag, b) exponential, and c) plateau phases (Catford et al. 2016). The lag phase is categorized by low population densities and slow rates of spread, and are typically followed by an exponential phase of rapid increase in range and population density. Eventually, invasive species reach a saturation phase, where population sizes stabilize. The duration and rate of change in these phases differ across species, and are often associated with invasiveness (Osunkoya et al. 2021). Overall, this information allows us to determine important dimensions of invasiveness: range size and spread rate, both of which can be used to assess the current and potential impact of invasive plant species.

Although range size is widely used as a proxy for potential impact and invasion success, it is important to recognize that it is one of the many dimensions of invasiveness (Catford et al. 2016). Species have various demographic (range size, habitat breadth, local abundance and spread rate) and impact dimensions (per capita impact) associated with their invasion potential (Catford et al. 2016; Parker et al. 1999). Using only range size for assessing the impact of invasive species assumes that range size is correlated with other dimensions of invasiveness. However, species with similar range sizes can differ in local abundance, or per capita effect, and therefore differ in their overall impact in a region (Liao et al. 2020). Field based studies can be used to quantify other dimensions of impact, like local abundance and per capita effect (Bernard et al.2019). However, such studies are resource intensive and therefore usually restricted to a few species, or to a smaller geographic area. An alternate approach to assess the impact of invasive species that is can incorporate the various dimensions of invasiveness is by soliciting expert opinions (Randall et al. 2008). Such questionnaire based surveys have the additional benefit that they can be modified depending on the focus of the impact being assessed (environmental vs. socio-economic impact) and the stakeholders being interviewed (Turbé et al. 2017). Such questionnaire based surveys can be used to determine an overall score that combines multiple aspects of invasion that can be used to prioritize invasive species for management (Morse et al. 2004).

The prominent knowledge gap in identification and prioritization of invasive species has been recognized globally, and steps necessary to rectify this have been identified by the Convention for Biological Diversity (CBD) (CBD 2000; Bacher et al. 2024). The CBD outlined the Aichi Biodiversity Targets in 2010, one of the goal of which was to identify and prioritize alien

invasive species for control and eradication, and prevent their reintroduction and establishment. The success of this was mixed across the globe, and in India, a few initial but important steps were taken towards establishing a list of invasive species and developing methods to prioritize these (Sandilyan 2019; Pant et al. 2021; Gulzar et al. 2024; Sankaran et al. 2021; Khuroo et al. 2021). There is only one study that has prioritized major invasive species based on their impact, but this only included a few major invasive species from the Indian subcontinent (Mungi et al. 2019).

The Western Ghats, one of the 34 global biodiversity hotspots (Myers 1988), represents only 5 % of the land area, but harbors 30 % of total species in the Indian subcontinent . In addition to the high diversity, over 15% of the plant species are endemic to this region (Deepu et al. 2023). At the same time, this region also hosts very high human population densities, and faces immense anthropogenic pressures (Gadgil and Malthotra 1982). The Western Ghats is divided into three regions: The Northern, Central, and Southern Western Ghats. The northern parts of this mountain range differs from its central and southern counterparts as it has lower mean annual precipitation and higher seasonality. The Northern Western Ghats is a centre of rapid diversification for many herbaceous genera (Shigwan et al. 2020). Studies on invasive plant species from the Western Ghats are either restricted to species inventories of restricted spatial scales (Ghate and Vartak 1990; Rao and Sagar 2012) or impact assessments of few species on single land use type (Patil and Janarthanam 2013; Joshi et al. 2020). A few of the multi-species studies from across habitats are restricted to species inventories and checklists .There is an urgent need to go beyond these species inventories and get a more comprehensive understanding of the invasive plants from Northern Western Ghats and the adjacent narrow belt of Konkan (Figure 1).

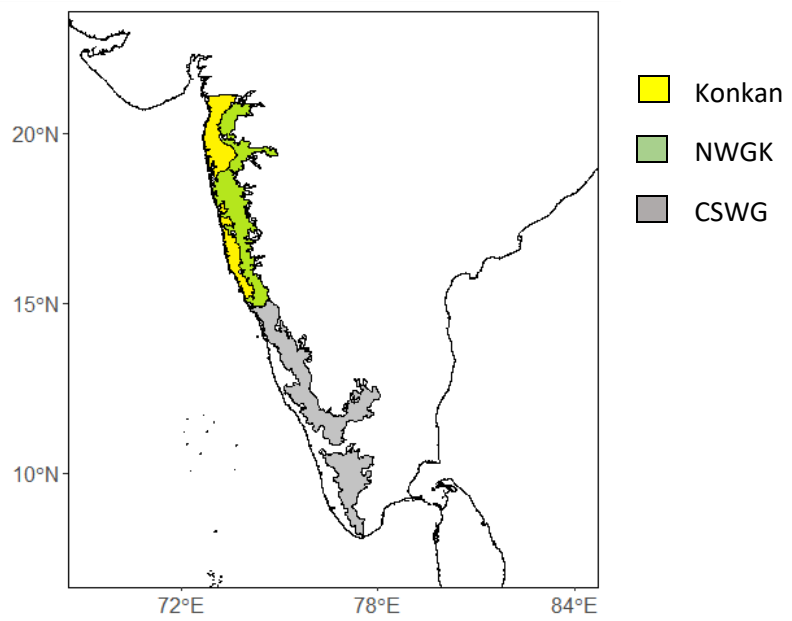

Figure 1: Schematic figure representing the study region on the map of India. Shaded region is the biodiversity hotspot Western Ghats. Green region represents central and Southern Western Ghats (CSWG). Study region (NWGK) is shaded in green and yellow. Green region represents the Northern Western Ghats and yellow represents Konkan region.

In this chapter, multiple complementary approaches were employed to understand the demographic and impact dimensions of invasive plants in the Northern-Western Ghats and Konkan regions (NWGK). Invasive plants were defined as non-native plants that have expanded their range size, and have important ecological, social or economic impacts. Initially, the invasive plants of NWGK were identified. This was followed by using complementary approaches to evaluate the impact of these plants based on different dimensions of invasion. Subsequently, the two approaches were compared based on the relative ranking of species across the dimensions of invasiveness determined by the two approaches. Finally, the expert survey based approach was used to assign overall rank to species across various dimension of invasion. These ranks were then used to identify high priority invasive plants of NWGK.

Methods

Identification of the potential invasive plants in NWGK

Three studies that had identified invasive and naturalized species in India (Sandilyan 2019; Reddy 2008; Inderjit et al. 2018) were used to compile a list of alien species which were invasive in any part of India, or naturalized in Maharashtra and Goa, the two states in which the Northern Western Ghats and Konkan regions are found. A comprehensive search was undertaken to confirm species that were not native to India. This list of confirmed non-native species was used by a core group of experts to identify species that were present, and problematic in the NWGK region. This resulted in the final list of seventy eight plant species that were identified as invasive to this region and used for further analysis (Appendix 1, 2).

Herbaria and literature based range size estimation

The collections for these seventy eight species from the four major herbaria of the region (Appendix 3) were accessed to extract information for the date and location of the collection. The data from the herbaria were supplemented with occurrence records from the Global Biodiversity Information Facility (GBIF) database (GBIF.org on 2021-08-04), from publications, and from twenty eight regional Floras (Appendix 4). To control for any temporal or spatial bias associated with sampling effort (Delisle et al. 2003), occurrence data were also collected for thirty three phylogenetically diverse native plants having similar life forms as the invasive plants (Appendix 5). Latitudinal and longitudinal co-ordinates of these occurrence points were determined using google maps. Based on previous studies and knowledge of spatial resolution of sampling effort from this region, 10 km^2 grids were laid on the shapefile of the NWGK region (Williamson et al. 2005; Antunes and Schamp 2017). Occurrence points were plotted on the

NWGK map using the 'sp package' in R (Pebesma et al. 2024). Range size was estimated by quantifying the number of 10x10km^2 grids occupied by each species.

A land-use land-cover (LULC) map for India (Roy et al. 2015) was used to quantify invasion pressure, defined as the number of invasive plant species in the different LULC categories in this region. The original map with a 100 m^2 resolution was converted into a coarser map with 10 km^2 grids to match the occurrence data for the invasive species. The modal LULC category with highest number of pixels was assigned to the coarser 10 km^2 grids. When the percent difference between highest and next highest LULC was less than 25%, both of the dominant LULC categories were assigned to the 10 km^2 grids. The total number of invasive plant species in each LULC category was determined. To control for differences in the proportional area occupied by the different LULC categories, the expected number of invasive plants given the area occupied by each LULC category was determined by a randomization exercise that was repeated 200 time. Differences between the observed and expected number of invasive plants in each LULC category was tested using a chi square test of independence.

Temporal dynamics

Analysis of the temporal dynamics of invasion was restricted to thirty eight species that were not cultivated, and were present in more than 15 grids (Osunkoya et al. 2021). The occurrence dates were binned at a decadal level, and the residence time, lag duration, spread rate, and spike function determined for species (Figure 2). Spike function represents the number of times a species has increased rapidly in a region given its residence time and is related to overall spread of the species (Osunkoya et al. 2021). To control for differences in sampling effort across time,

the number of grids occupied by each invasive species was divided by the number of grids occupied by all native species at that time point. The cumulative log ratio of the grids occupied by invasive species divided by the grids occupied by native species was plotted as a function time. Segmented regressions were used on the resultant invasion curves to identify inflection points, the regions of distinct changes in the rate of increase (Osunkoya et al. 2021). The time passed since the species' first report was used to estimate the residence time. The duration between first reported date and the first inflection point with no/slow growth rate was used to estimate lag duration (Figure 2). To estimate the spike function for a species, the number of time points with a higher number of records for the invader than natives was determined. This was divided by the residence time for that species to determine the spike function. Spread rate was estimated as both the overall slope of increase over time and the maximum rate of increase over time. These temporal parameters along with intrinsic species properties such as lifespan and life-form are known to be associated with invasion success (Osunkoya et al. 2021). Using range size as a proxy for invasion success, a GLM was performed with range size as the response variable, and lifespan, life-form, and estimates of temporal dynamics as predictor variables. Since the response variable was count data, negative binomial generalized linear model (GLM) was performed using the R package 'MASS', version 7.3- 58.3 (Ripley et al. 2024).

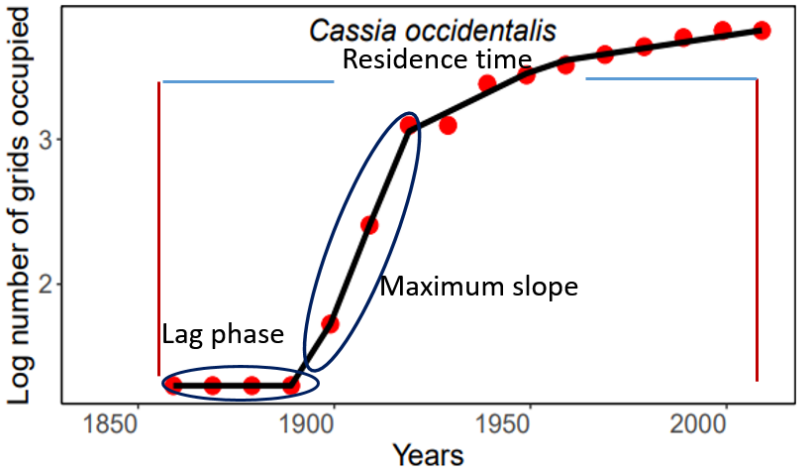

Figure 2: Temporal change in spatial distribution of a species. Representative species shows the change in geographical extent of *Senna occidentalis* measured as the number of grids occupied by the species in each decade controlled for the sampling effort during the time frame. Different temporal parameters such as residence time and lag phase of the species has been highlighted. Vertical lines mark the dates of first and last report of the species in the region, the entire region between these time points marked with horizontal line is the residence time of the species.

Expert based approach for demographic and impact dimension

A questionnaire-based expert opinion survey was conducted to complement the information obtained from the herbarium based approach described above, and more comprehensively understand other dimensions of impact of invasive species in this region. Fifty-five species with the highest range sizes based on the occurrence data were selected for this exercise. Thirty one plant ecologists and field biologists with extensive field experience in the NWGK region were identified for the interviews (Appendix 6). The expertise of this group ranged from ecology and taxonomy to conservation and management, and the years of experience in the field ranged from 10 to more than 30 years. Care was taken to include experts from diverse geographic areas representative of the NWGK region.

The questionnaire consisted of six primary questions focused on the distribution and ecological impact of these species (Morse et al. 2004). These questions were selected as they provide information on the major demographic and impact dimensions of invasiveness. An additional three open-ended questions were included to identify emerging invasive species, any other invasive species that may not have been identified in the initial process, and any invasive species that was problematic but the impact of which has currently reduced (Appendix 7).

Since expert based approach provides contemporary and comprehensive information of different dimensions of invasiveness, I used this approach to estimate overall impact of invasive plants. The six primary questions were converted to a unidirectional four-point Likert scale (Likert, 1932), which allowed the summation of scores to determine a cumulative impact score for each species from the modal responses of the experts. Modified Braun-Blanquet cover-abundance (BBCA) categories were used (McNellie et al. 2019) to convert continuous responses for questions on range size and local abundance to an ordinal scale. To quantify habitat breadth, species were marked as present in a particular habitat if more than 20 % of the experts had reported the presence in that habitat. All the modal scores were provided with a confidence value. Multinomial confidence intervals were estimated using the R package 'MultinomialCI' package (Villacorta 2021). The scores across likert scale objects can be summed only when they validate the assumptions associated with internal consistency and dimensionality. Tests for internal consistency between the questions were performed using Cronbach's alpha analysis (Jebb et al. 2021). PCA was performed to test the dimensionality of the questions. Since the Cronbach's alpha value was 0.8106, and questions were unidimensional, scores obtained for the

species were added across different questions to obtain cumulative score for each species. These scores were used to rank species and identify high priority invasive plants of this region.

Comparing different dimensions of invasiveness

To understand the relationships between the different dimensions of invasiveness a principal component analysis (PCA) was performed using the factoextra package (Kassambara and Mundt 2020). The relative rankings for range size, habitat breadth, local abundance, presence in protected areas, impact on biodiversity and current temporal trend obtained from the expert survey, and for range size determined from the herbarium based approach for 55 species were included in the PCA analysis. A second PCA analysis was performed where information from the temporal analysis, namely lag length, rate of spread, and residence time were also included. This second analysis was restricted to the 38 species for which this additional information was available. Further, I also explored the relationship between species rank based on range size obtained through herbaria and questionnaire. For herbaria both overall range size and range size in natural areas (excluding occurrence in buildup area and plantation-agriculture LULC type) was quantified. Spearman's correlation was performed to test the strength and significance of this relationship.

Results

Identification of the potential invasive plants in NWGK

Out of the 347 non-native naturalized or invasive plants of the Indian subcontinent, 282 were identified by a core group of experts to be present in the Northern Western Ghats and Konkan

regions (NWGK). Of these 282 species, 78 species (approximately 25% of the naturalized species) were identified by the experts as invasive (Appendix 8, 9).

Range size

There was a huge variation in range size of invasive plants obtained in this region. There was an order of magnitude of variation between the species with the smallest and largest range size. The distribution of range sizes was highly skewed with only 15% of species being highly widespread (Figure 3) that is they had occupied around 20% of the total studied region of NWGK.

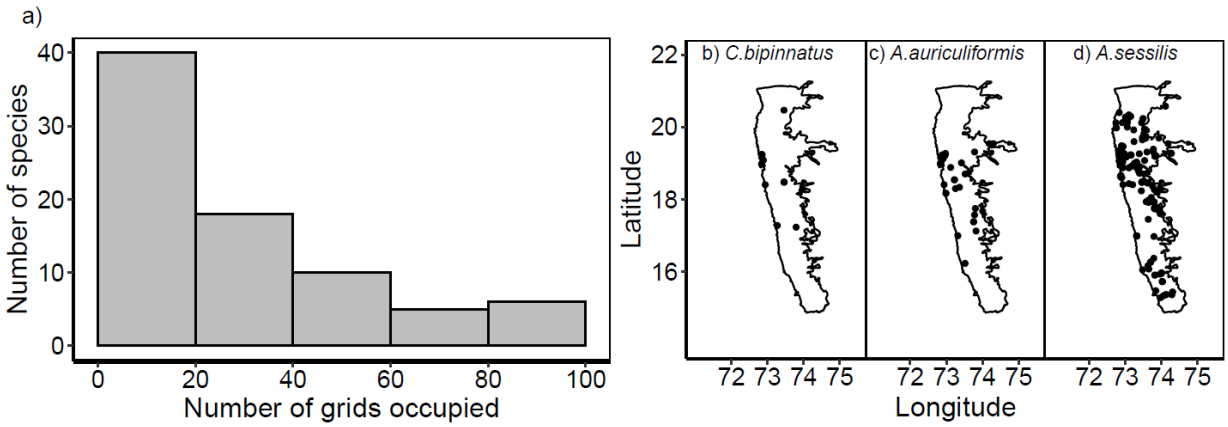

Figure 3: Range size of the invasive plants of Northern Western Ghats and Konkan region (NWGK). a) Histogram of number of grids occupied by species showing variation in number of species occupying number of grids. Representative examples of species with: b) low, c) medium and d) high range size in the study regions.

Croplands and deciduous forests were found to host the highest number of the invasive plant species in this region. However, both these LULC types had disproportionately large number of area in this region. After controlling for the differences in the area occupied by each LULC type a significant difference was found between expected and observed number of invasive plants across LULC types ($p < 0.001$). Human habitations and mangroves had significantly higher pressure of observed invasive plant species, whereas miscellaneous areas which were

characterized by open canopy region with high anthropogenic pressure had significantly less number of invaders than expected. There was no significant difference between expected number of invasive plants and observed invasive plants in other LULC types (Figure 4).

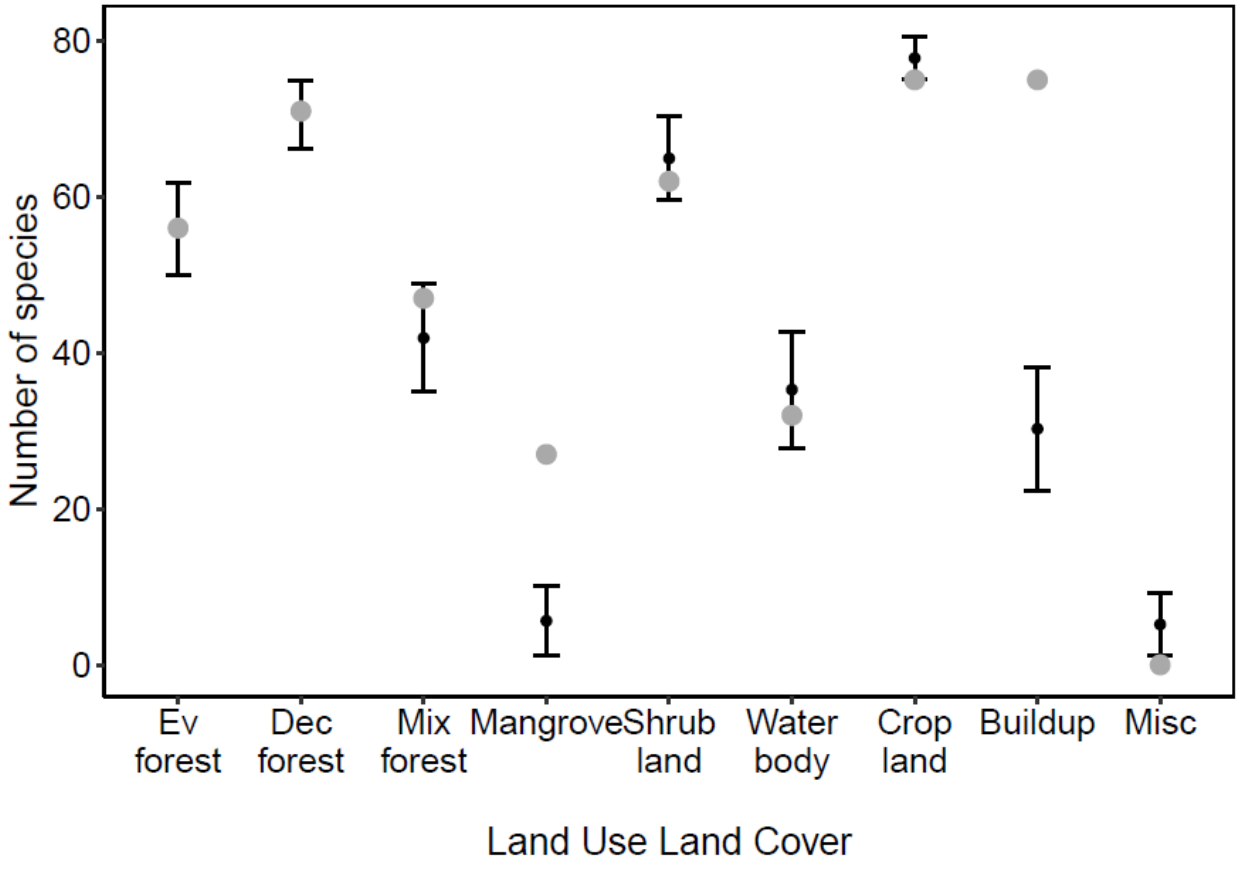

Figure 4: Number of invasive species present in different Landuse Landover (LULC) type found in NWGK. The black lines with points represent the mean and standard deviation of expected number of invasive species present in each LULC type calculated across two hundred randomization. The gray point represent the observed number of invasive species in each LULC type. Misc represents miscellaneous lulc group which includes open canopy region with high anthropogenic pressure

Temporal dynamics

Different temporal patterns were observed amongst the thirty eight invasive species in the NWGK. (Figure 5). There were four main predominant patterns: Species with distinct lag, which

are showing reduction in spread rate in recent decades (~30%), species with distinct lag and rapid spread rate (~7%) , species with no lag but reduction in spread rate in recent times (~30%) and species with no lag and rapid spread rate (~30%). Overall 40% of the species had a distinct lag and one-third of the invasive plants showed no signs of reduction in spread rate in the recent decades.

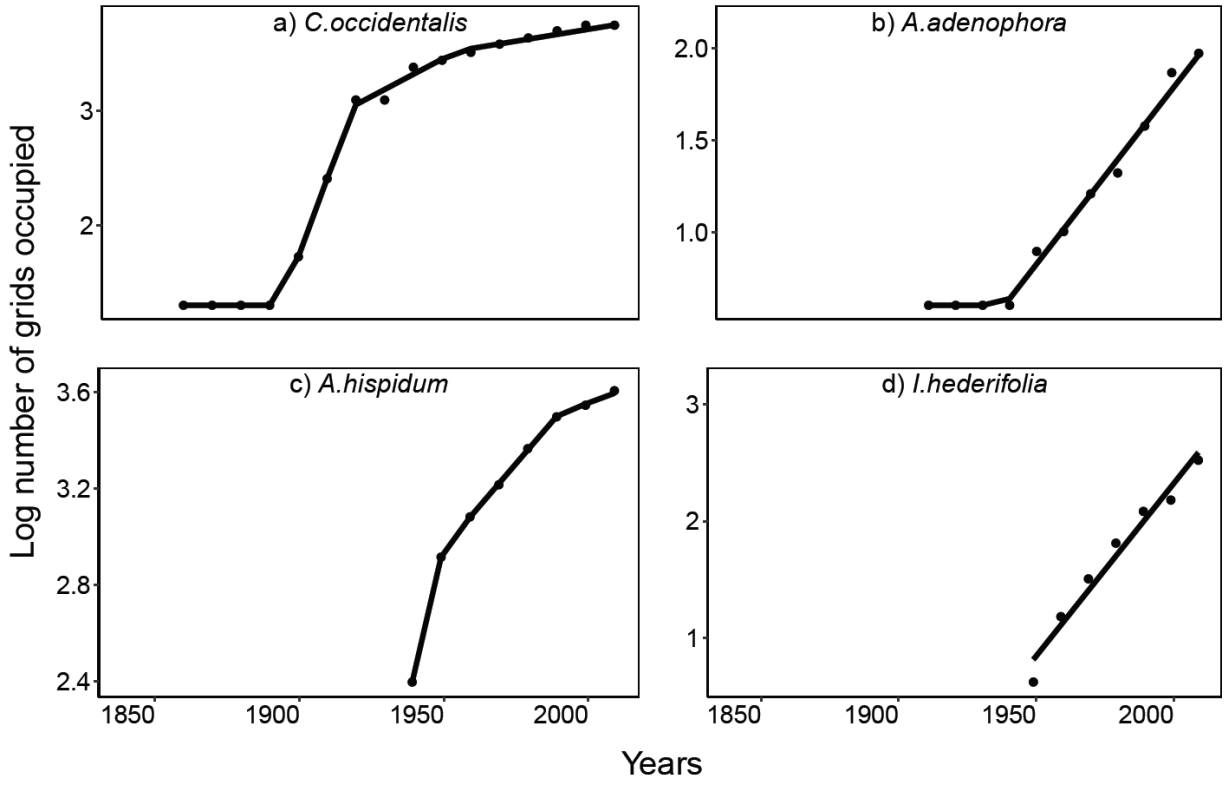

Figure 5: Representative examples showing variation observed in pattern of their spatial distribution over time. a) Species with distinct lag, increase and saturation, b) species without saturation, c) species without lag and d) species with neither lag nor saturation.

The distribution of lag lengths was right skewed with half of the species showing no detectable lag. For over 90% of the studied species, lag lengths were in the range of 0-40 years (Figure 6a). Interestingly, *Chromolaena odorata* had an exceptionally long lag length of 138 years. Spread rate of species had an unimodal distribution with most species having spread rate of 0.012 grids/year in the region (Figure 6b).

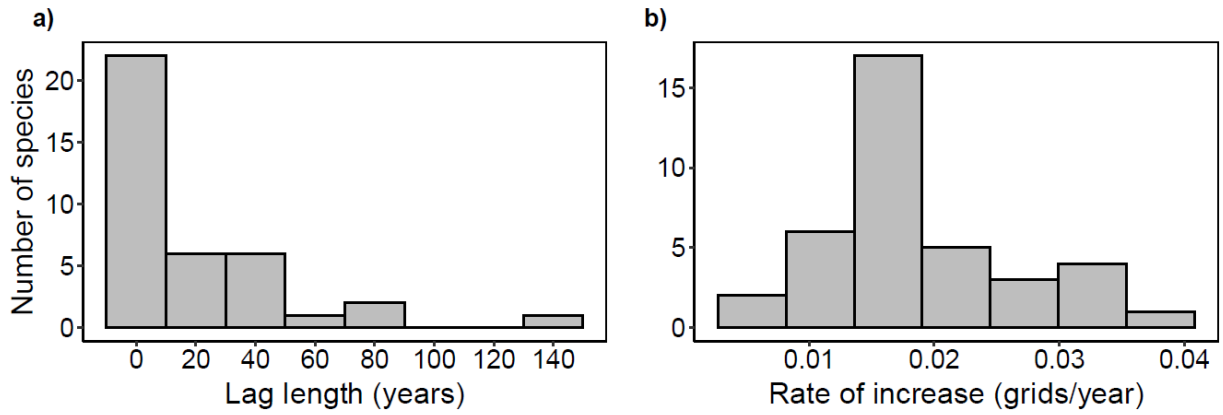

Figure 6: Variation in different temporal parameters within the invasive plants of NWGK. a) Histogram showing distribution of species with different lag lengths. b) Histogram of species having different rates of increase across time. The height of bar represents number of species in each lag length or increase rate class.

While comparing the various measures of temporal dynamics with range size, residence time ($p<0.001$) was found to be positively and lag length ($p <0.05$) was found to be negatively associated with the range size of species. There was a marginal association ($p = 0.06$) between lifespan (intrinsic species property) and range size. Annual species had larger range size than perennial species (Table 1).

Table 1: Table showing relationship between different temporal parameters- overall slope, length of lag phase, residence time and intrinsic species trait lifespan and lifeform with total number of grids occupied by the species.

Temporal parameters	**Grids occupied**
Spread rate	ns
Length of lag phase	-
Residence time	+
Spike function	ns
Growth form	ns
Lifespan	Annual > Perennial

Expert based approach for demographic and impact dimension

Based on the responses from experts for the fifty-five invasive plants, I identified that most species had medium range size and only very few had high range sizes in this region. Several species had very low to low range sizes (Figure 7a). Although, majority of the invasive plants did not show any major change in their range sizes in the last 30 years, 15% of the species showed an increasing trend (Figure 7b). *Parthenium hysterophorus* an extremely problematic invasive species seems to be in decline in this region. With respect to habitat breadth, most of the invasive plants were present in three or more habitat types. Very few of these species were reported to be found in very specialized habitats (Figure 7c). These habitat specialists were *Eclipta prostrata, Ipomoea carnea, Monochoria vaginalis* and *Typha domingensis*. The local abundance distribution was highly skewed with majority of the species present at very low and low local abundances. Around 30% of the species had medium or high local abundance (Figure 7d). Around half of the invasive plants were reported to be present in protected areas of this region, but mostly in the disturbed portions (Figure 7e). Only *Chromolaena ordorata* was reported by the experts to be present in the invaded or undisturbed regions of protected areas. Around half of the invasive plant species were reported by experts to have negative impact on the native biodiversity of NWGK (Figure 7f).

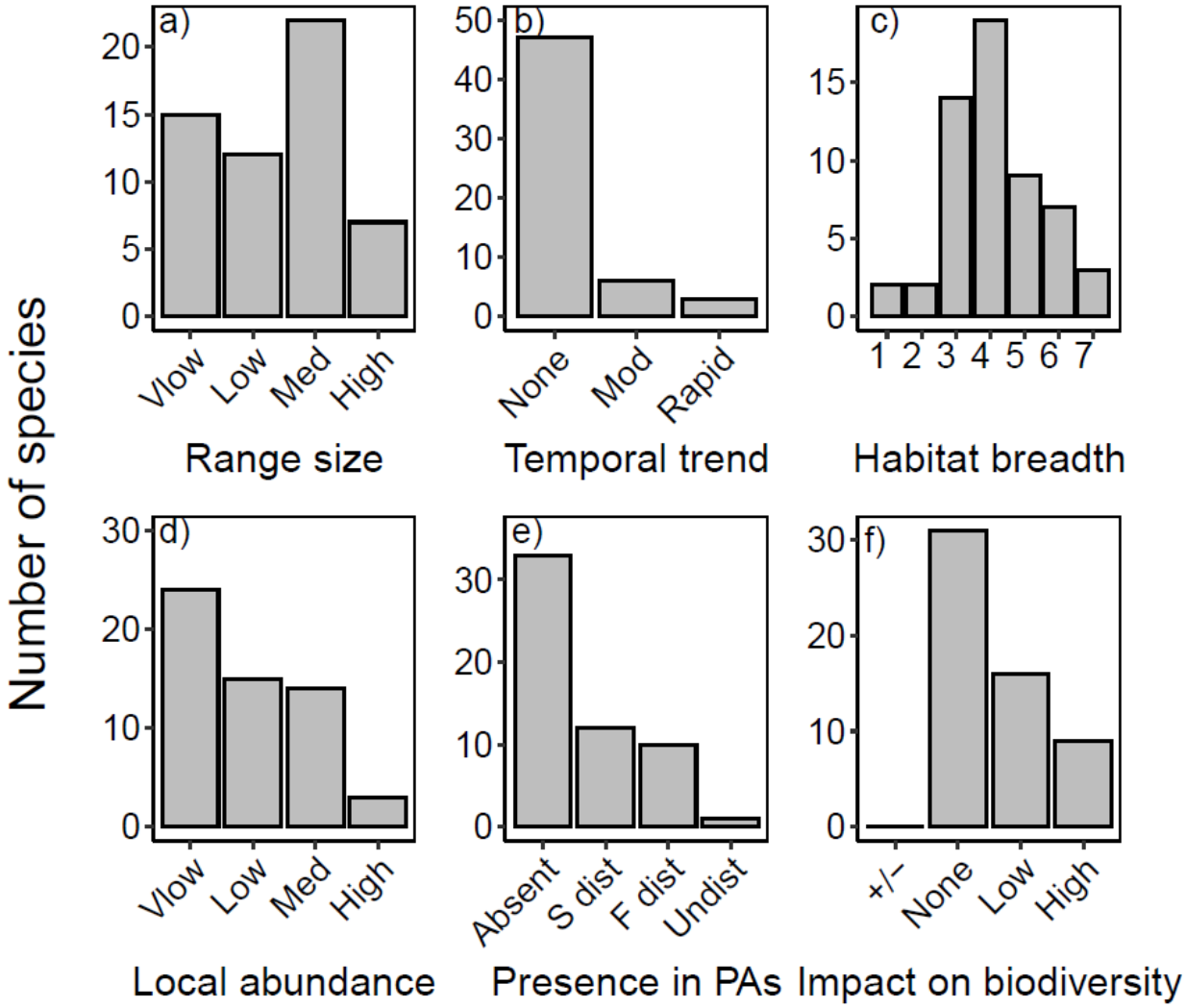

Figure 7: Distribution of Invasive plants along different dimensions of invasion obtained through questionnaire based approach. Species have variation in different aspects related to range size, a) total range size, b) rate of increase in range size over time and c) number of habitats occupied e) presence of species in protected area with different levels of disturbance. d) Number of species in each abundance class, an important demographic dimension of invasion and f) number of species having different levels of impact on the native biodiversity. Vlow- very low, Med-medium, Mod-moderate, S dist- sometimes in disturbed area, F dist- frequently in disturbed area, Undist- Undisturbed area.

Comparing different dimensions of invasiveness

The dimensions of invasiveness of these species, obtained using the two approaches (herbaria and experts) were compared. The first two dimensions explained sixty three percent of the variation observed. Responses from all the questions had higher loading on PC1 except for habitats occupied and impact on biodiversity which loaded on dimension 3 and dimension 2 respectively. Range size obtained from herbaria had a higher loading on the second dimension (Figure 8, Appendix 10, 11). Species had comparable behavior on abundance and range size dimension. Similar results were found when PCA was performed for a smaller set of species including by including other temporal parameters (Appendix 12, 13) .Interestingly, range size estimates obtained from herbaria and experts were only partially related (Figure 9). This relationship was true even when herbaria data was used to quantify range size restricted to natural areas only ($r = 0.42$, $p < 0.001$).

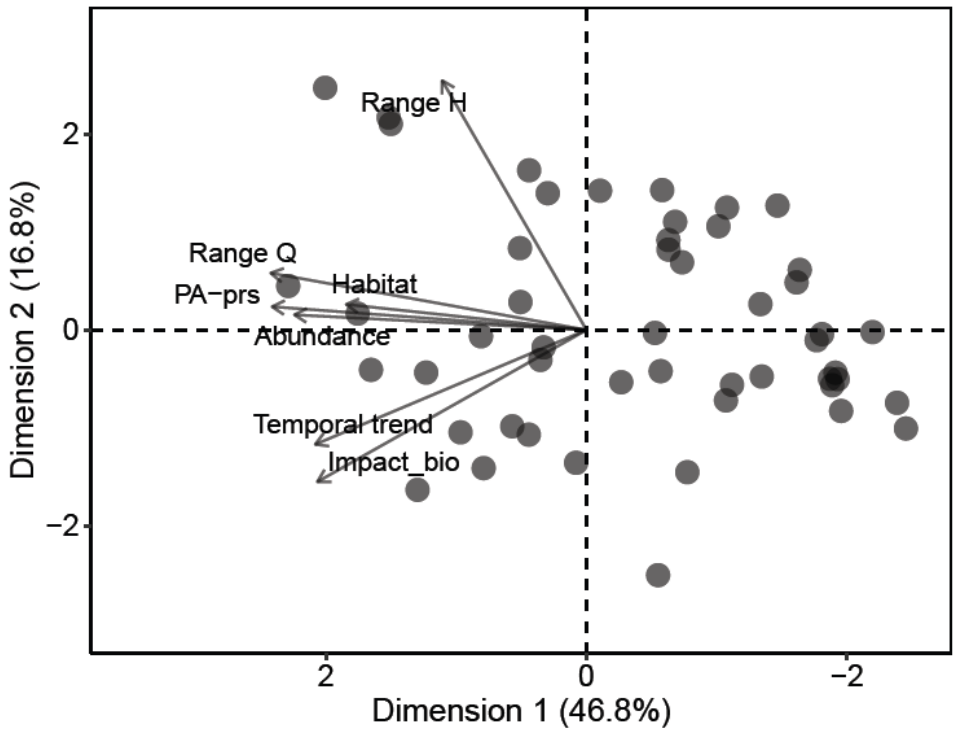

Figure 8: Rank of species along the different dimensions of invasion obtained through two distinct complementary approaches i.e. herbaria and questionnaire. The graph shows principal component analysis for seven aspects of invasion. The first two PC explains 63% of variation in the data. Herbaria range size has higher loading on PC2 whereas other dimensions of impact and abundance have higher loading on the first PC dimension. Range H- range size herbaria, Range Q- range size questionnaire, Habitat- habitat width, PA-prs- presence in protected areas, Abundance- local abundance, Impact_bio- impact on biodiversity.

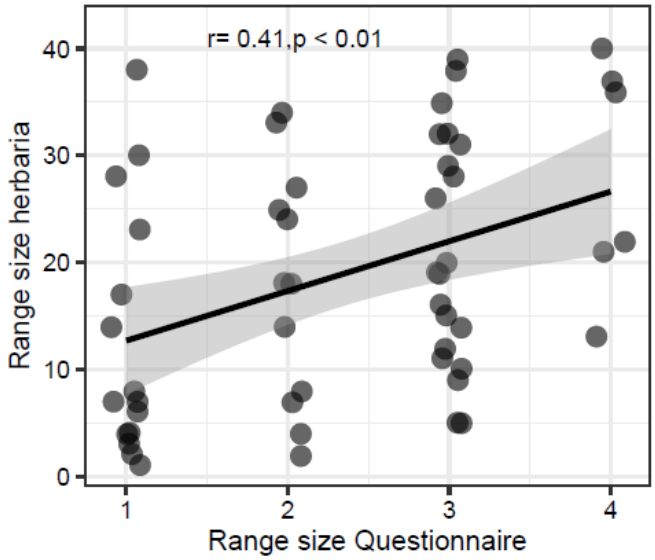

Figure 9: Correlation between rankings of species based on their range size, as determined through herbaria data and questionnaires. The herbaria-based ranking was calculated by estimating the absolute number of occupied grid for each species. Points in the figure represent invasive plants in NWGK. The line represents a type I regression, with the shaded region indicating the 95% confidence interval

Identifying high priority invasive plants

The distribution of scores obtained across different dimension of was highly skewed with most species having low overall scores and only few species having very high scores (Figure 10). These scores were used to provide an overall rank to species which was then used to identify high priority invasive plants. Six species *Chromolaena odorata, Mesosphaerum suaveolens, Cosmos sulphureus, Alternanthera ficoidea, Lantana camara* and *Synedrella nodiflora* were identified as high priority invasive plants of this NWGK. No additional species were identified by experts as currently invasive in the region. However, from open ended questions *Senna uniflora, Gliricidia sepium,Tecoma stans, Ipomea paracitica, Mikania micrantha* and *Physalis peruviana* were identified as emerging invaders of NWGK.

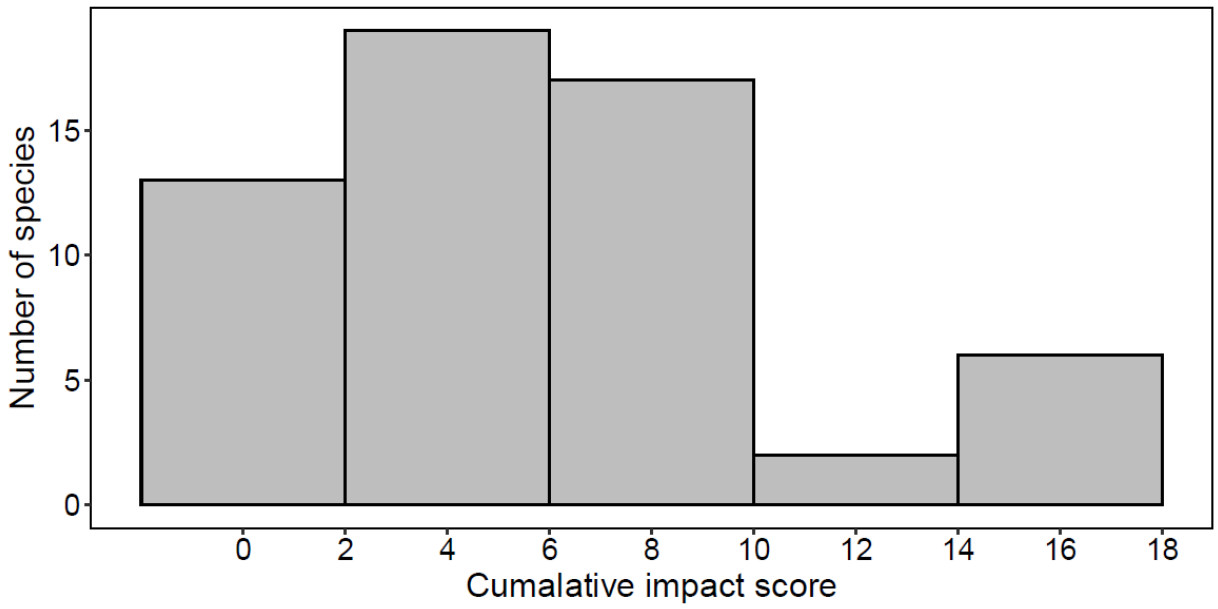

Figure 10: Distribution of cumulative impact scores of invasive plants of NWGK. Cumulative scores were obtained by summing scores across various dimensions of invasiveness obtained through questionnaire-based expert opinion survey based approach

Discussion

This study identified 282 non-native naturalized plant species from the Northern-Western Ghats and Konkan regions. Out of these, seventy-eight species were classified as Invasive to this region. Two complementary approaches were used to identify the different dimensions of invasiveness for these species. Results showed that only a few species had high impacts across the different dimensions. Range size estimated through herbaria showed a huge variation with only around 15% of the invasive species having large range sizes. Expert based approach, was used to gather information on other demographic and impact dimensions of these invaders. Around one third of the species had medium to high local abundance and half of the invaders showed large habitat breadth. On the impact dimension, only half of the invaders were found to be present in the protected and had a negative impact on biodiversity. Finally, six species with high overall scores across all dimensions, were identified and classified as high priority species.

These species are noxious weeds that must be controlled and prioritized for management in NWGK.

India has a total of 450 naturalized plant species out of which, 282 plants are found in NWGK. Despite its small size relative to the entire subcontinent, NWGK hosts 50% of naturalized plants of the country. Seventy-eight of the 282 plants were invasive in NWGK. Number of invasive species in a region may relate to the area, with larger region having more invaders than smaller region. However, factors other than area can determine the number of invasive species a region supports (Bhatta et al. 2023). Therefore, it's better to evaluate the ratio of invasive to naturalized species in a given area. According to ten's rule, ten percent of all the naturalized species become invasive in a region (Williamson and Fitter 1996). However, our results show that approximately 25% of the naturalized species are invasive in NWGK. This aligns with recent research highlighting that the ratio of naturalized to invasive species often exceeds the ten percent estimate, with studies suggesting an average of 25% of naturalized plants can become invasive (Jeschke and Heger 2018).

Range size of invasive plants obtained from herbaria showed a huge variation in range size of invasive plants in this region. Only 15% of these plants are highly widespread. Such observations are not uncommon as invasive plants have different axis of invasiveness. Often times species might not become spatially widespread but can still be a problem due to their high local abundance (Fristoe et al. 2021). Distribution data obtained from herbaria are helpful not just in determining species range size but can also be used to identify LULC types with high invasion pressure. Mangroves and human habitats of NWGK had significantly higher number of invasive

species than expected by their area. Presence of high number of invasive plant species in human habitation is not surprising as frequent introductions, human mediated dispersal, empty niches and disturbed landscapes, found in human habitats help these species to thrive (Hierro et al. 2006). Studies have shown that disturbances especially the raised lands of mangroves are associated with successful establishment of introduced species (Biswas et al. 2018).

Another, important dimension associated with invasion is the spread rate of an invader. With the help of herbaria data, I gathered information on spread rate and other aspects of temporal dynamics of these invasive species. Although two thirds of these invaders have slowed down in recent decades, none have yet attained saturation. In addition to spread rate, herbaria data also provided information on lag lengths and residence times of invasive species. Invasive plants in NWGK had lag periods of 0-40 years, which is similar to what has been previously shown from the tropics (Daehler 2009). Furthermore, species with shorter lags were the ones with large range sizes. This was expected as species with shorter lags can quickly overcome the biotic resistance and become widespread in a region (Larkin 2012).

Expert responses often provide contemporary insights into the demography and impact dimension of invasiveness. Species were related along many of these different dimensions. Species distribution across most of the dimensions were skewed with very few species having higher values and majority of species having row values on these dimensions. Even though the results showed that majority of the invasive plants had low ranks across these dimensions, I emphasize that this study was restricted to current environment and land-use conditions. Species

which are range restricted or less abundant can become a problem under the rapidly changing environmental and land-use conditions (Bellard et al. 2013).

One of the most crucial demographic dimension associated with invasion is local abundance (Catford et al. 2016). According to experts, one-third of the species show moderate to high local abundance in NWGK. High abundance are along with range size and per capita impact, are directly associated in overall impact of the invader (Parker et al. 1999). Additionally, majority of the species were present in multiple habitats. This shows that the invasive plants of NWGK have wide bioclimatic tolerance ranges. Furthermore, according to experts, only 15% of the invasive plants have actually increased in the recent past. Interestingly a major invader of Indian subcontinent *Parthenium hysterophorus* which showed rapid spread rate, is now decreasing in this region according to experts. This could be due to competitive exclusion by emerging invasders like *Senna uniflora* and *Mesosphaerum suaveolens* (Kumari et al. 2010).

Experts also provided information on the impact dimension of these species. Impact was estimated by evaluating their presence inside the protected areas and direct impact on biodiversity. Only half of the species were present inside protected areas and caused negative impact on biodiversity. Except *Chromolaena odorata*, all of them were found only in the disturbed portions of the protected areas. Our result is consistent with the other studies that show that protected regions can resist the establishment and impact of invasive species (Mungi et al. 2021). The findings align with the biotic resistance hypothesis, which suggests that invasive species fail to establish themselves in areas that are rich in species and have strongly interacting native communities (Elton 1958).

In this study I used two methods (herbaria and expert) to obtain range sizes of species. Although herbaria is a vital and invaluable source of occurrence data, there a few limitations of using this historical data to understand the current distribution of species. Therefore species' range sizes were also quantified based on information provided by experts. Although range size information obtained by both methods was similar for 40% of the species, I did find that herbaria underestimated range size for species which are introduced recently and are in their increase phase. This can happen because herbaria collections are often associated with time lags, which can hinder our ability to grasp recent trends in species distribution (Hyndman et al. 2015). Despite the differences in range size of individual species, overall both methods show that only a very small proportion of invasive plants are widespread in this region

Herbaria and expert based approach were the two complementary methods used in this study to understand different demographic and impact dimensions of invasive plants of NWGK. Herbaria based approach provided information on range size, spread rate and other temporal dynamics of the species. Whereas the expert based approach was used to get information on impact and local abundance of species. Although both these methods are frequently used, issues of associated with both of these methods are well recognized. Herbaria data are often limited and have biased collection of certain type of species more than the others. Although to control for such biases, I have used widespread native species as a proxy for sampling effort, this may not always be enough. To get a more robust control against spatial and temporal bias, all the species in the herbaria must be studied (Antunes and Schamp 2017). Another limitation of herbaria are the time lags in species collection, which can range from few years to decades (Hyndman et al. 2015). These lags can limit the current understanding of species. On the other hand, use of expert

opinion to study other dimensions of invasion is also not devoid of problems. These data often have strong observational and taxonomical biases (White et al. 2005). For example, major invasive species, might score high on every dimension of invasion because some experts might have strong bias against them. Additionally, even when unbiased, expert data can only be used to understand recent patterns/trend of species, to understand long term temporal dynamics of species (such as spread rate, minimum residence time) one must solely rely on herbaria data (Burni et al. 2024).

Prioritizing of species is important in order to direct the limited resources available for management (Mungi et al. 2019). Species prioritization protocol varies depending upon the sector (ecological vs. socio economic) on which impact is being studied. Since, our aim is to identify and manage species which are currently a problem, I used expert responses over herbaria data to identify high priority invasive plants of NWGK. I used different dimensions of invasion to identify high priority plant invaders of NWGK. Six species have critically high impact on the natural areas of this region and therefore must be prioritized for management during biodiversity conservation exercises. Three of these six species are also mentioned as the high priority invasive species for India (Mungi et al. 2019). Many invasive plants have very low overall scores. Finally, I also provide a list of emerging invaders which recent introductions but are rapidly spreading in NWGK. I propose conducting impact assessment studies on these species to develop an efficient strategy for management and control.

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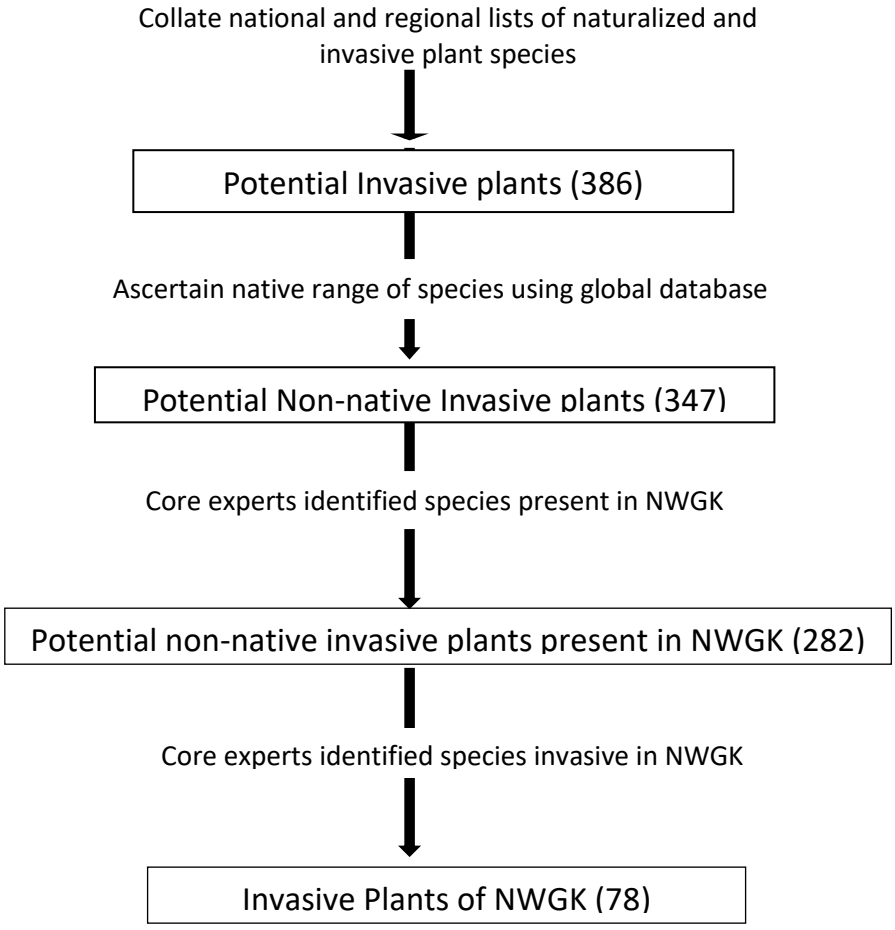
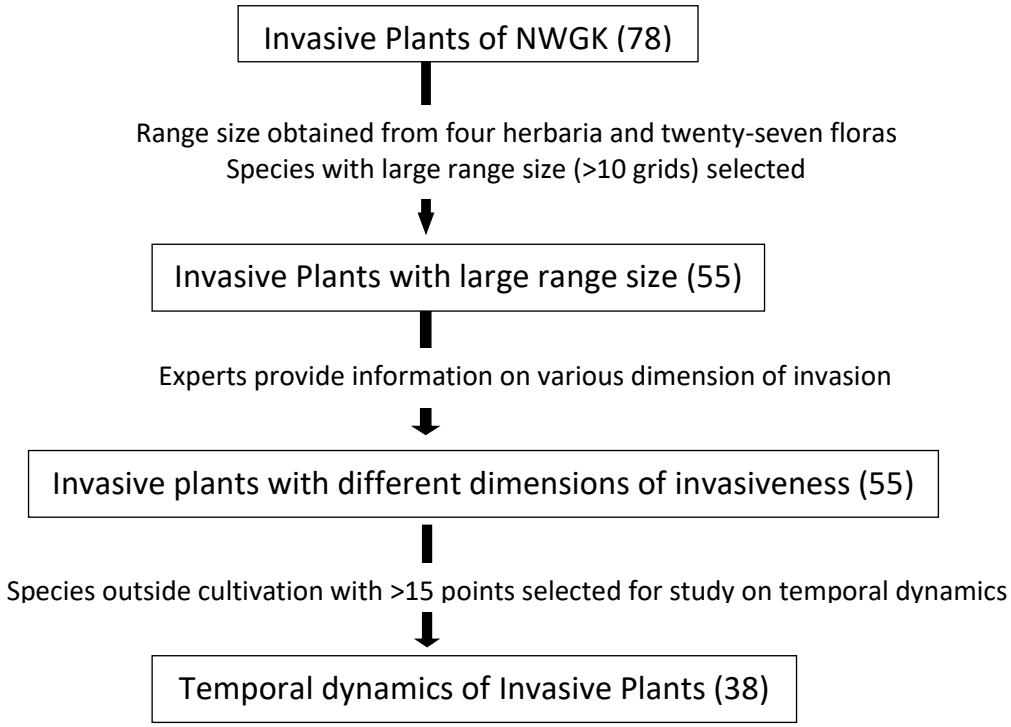
Appendix 1: Flowchart describing steps of identifying invasive plants of the Northern Western Ghats and Konkan regions (NWGK)



Appendix 2: Flowchart describing steps of selecting species for herbaria based and questionnaire based approach to quantify different dimensions of invasiveness



Appendix 3: Details of herbaria referred for spatial and temporal analysis of invasive plant species

S.no.	Name	Year of establishment	Abbreviation	Number of specimen	Area of collection
1	Botanical Survey of India Herbarium, Western regional centre, Pune	1955	BSI	1,79,000	Daman & Diu, Dadra & Nagar Haveli, Maharashtra, Goa and Karnataka
2	Blatter Herbarium, St. Xavier's College, Mumbai	end of 19thce	BLAT	1,50,000	Maharashtra
3	Agharkar Herbarium, Agharkar Research Institute, Pune	1946	AHMA	33,000	Maharashtra
4	Shivaji University Kolhapur Herbarium, Kolhapur	1964	SUK	30,000	Southwestern Maharashtra, Northern Karnataka

Appendix 4: Reference of Flora used for spatial and temporal study of invasive plant species

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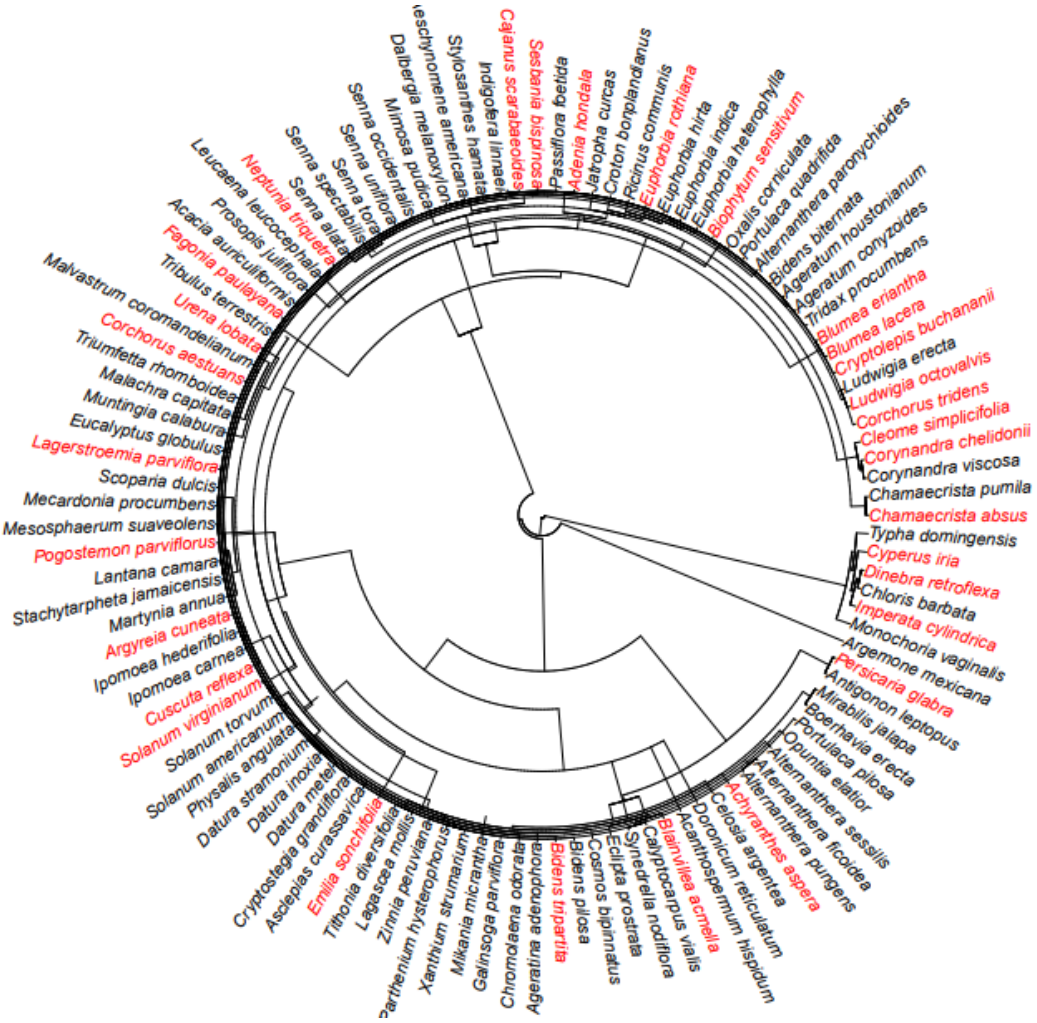
Appendix 5: Natives selected to control the sampling bias. The selected native species were uniformly distributed along the phylogenetic tree. Native species are in red, invasive plants are marked in black.



Appendix 6: Name and institutional affiliation of experts who participated in the interview

S.no	Expert name	Institutional affiliation
1	Alok Chorghe	National Museum of Natural History, Delhi
2	Anup Deshpande	Omni active health technologies, Mumbai
3	Aparna Watve	IUCN SSC Red list authority coordinator
4	Arun Prashant	Pune university, Pune
5	Arun Chandole	Abasaheb Marathe Arts and New Commerce, Science College, Rajapur
6	Ashish Nerlekar	Michigan state university, Michigan
7	Bhanudas Chavan	IISER, Pune
8	Ankur Patwardhan	Abasaheb Garware College, Pune
9	Sanjay Auti	H.P.T. Arts and R.Y.K. Science College, Nashik
10	B.G Kulkarni	Botanical survey of India, Pune (Retired)
11	Jagdish Dalvi	Botanical survey of India, Pune
12	M.K Janardhanam	Goa University, Goa
13	Jui Pethe	Independent researcher, Nashik
14	Ketaki Ghate	Oikos, Pune
15	Mandar Datar	Agharkar Research Institute ,Pune
16	Mayur Bhagwat	Indian Institute of Science, Bangalore
17	Mayur Nandikar	Naoroji Godrej Centre for Plant Research, Pune
18	Milind Sardesai	Pune university, Pune
19	Navendu Page	Thackeray wildlife foundation, Mumbai
20	Nilesh Malpure	Kopargaon College, Ahmednagar
21	Prajakta Pathare	AECOM, Mumbai
22	Praveen Kale	St. Xavier's college, Mumbai
23	Prerna Agrawal	Ecosphere, Pune
24	Rani Bhagwat	Baburaoji Ghaopal College, Sangvi
25	Rutuja Kolte	Govindram Seksaria Science College, Belgaum
26	Sharad Kamble	MVP arts science college, Triamakeshwar
27	Shrikant Inghalikar	Independent researcher, Pune
28	S R yadav	Shivaji University, Kolhapur (Retired)
29	Sushant More	Insititue of Science, Mumbai
30	Vinod Gosavi	HPT Arts and RYK Science, Nashik
31	Vinod shimpale	The new college, Kolhapur

Appendix 7: Questionnaire used for the interview- All the questions were later converted to a four point unidirectional Likert scale

Name of expert-
Date of interview-
Regional expertise-
Year you started working in the region-
Unique kind of landscapes or habitats types are there in your study area-
Taxonomic expertise-

Current Distribution:

1) When was the first time you observed the species in your area (approximate year)-

2) Percentage of your study area that the species occupies (Rough estimate)-

3) Number of the above mentioned landscapes or habitats in which species is found

4) What is the relative local abundance of a species (whenever it is present)?

Trend in Distribution and Abundance:

5) In your experience, have you observed local range expansion or change in abundance of the invasive species over time?

a) High significance- dramatic increase in the abundance in the area in which species occurs
b) Moderate significance-Moderate increase in the abundance in the area in which species occurs
c) Low significance- Species not changing its abundance in the area it occurs in
d) Insignificant- Species decreasing in abundance
e) I'm unaware-

6) Ability to Invade protected areas and other undisturbed habitats

a) High significance- Regularly establishes in undisturbed portions of intact or otherwise healthy, native vegetation (e.g.- Undisturbed forest patches)
b) Moderate significance- Regularly establishes in disturbed patches within forest/conservation areas
c) Low significance- sometimes establishes in disturbed patches within forest/conservation areas
d) Insignificant- Not known to spread significantly into conservation areas (Present only at forest boundaries)
e) I'm unaware-

Ecological impact:

7) Impact on community abundance

Direction- Positive (+) –> Causes increase in native biodiversity or species abundance;
Negative (-) –> Causes reduction in native biodiversity or species abundance (or increase in other exotics)

Magnitude- High (++/- -) –> Causes major impacts on multiple species
Low (+/-) –> Causes small or no changes for a few species

a) + + (High Positive impact)
b) + (Low Positive impact)
c) - - (High Negative impact)
d) - (Low Negative impact)
e) Species has both positive and negative impact on community abundance (Please mention the magnitude of both)
f) Species has no impact
g) I'm unaware

8) Name of non-native species which are emerging (last 2 decades) as a potential problematic species in the region.

9) Name of the current problematic major non-native invasive species from the region which were not in the list

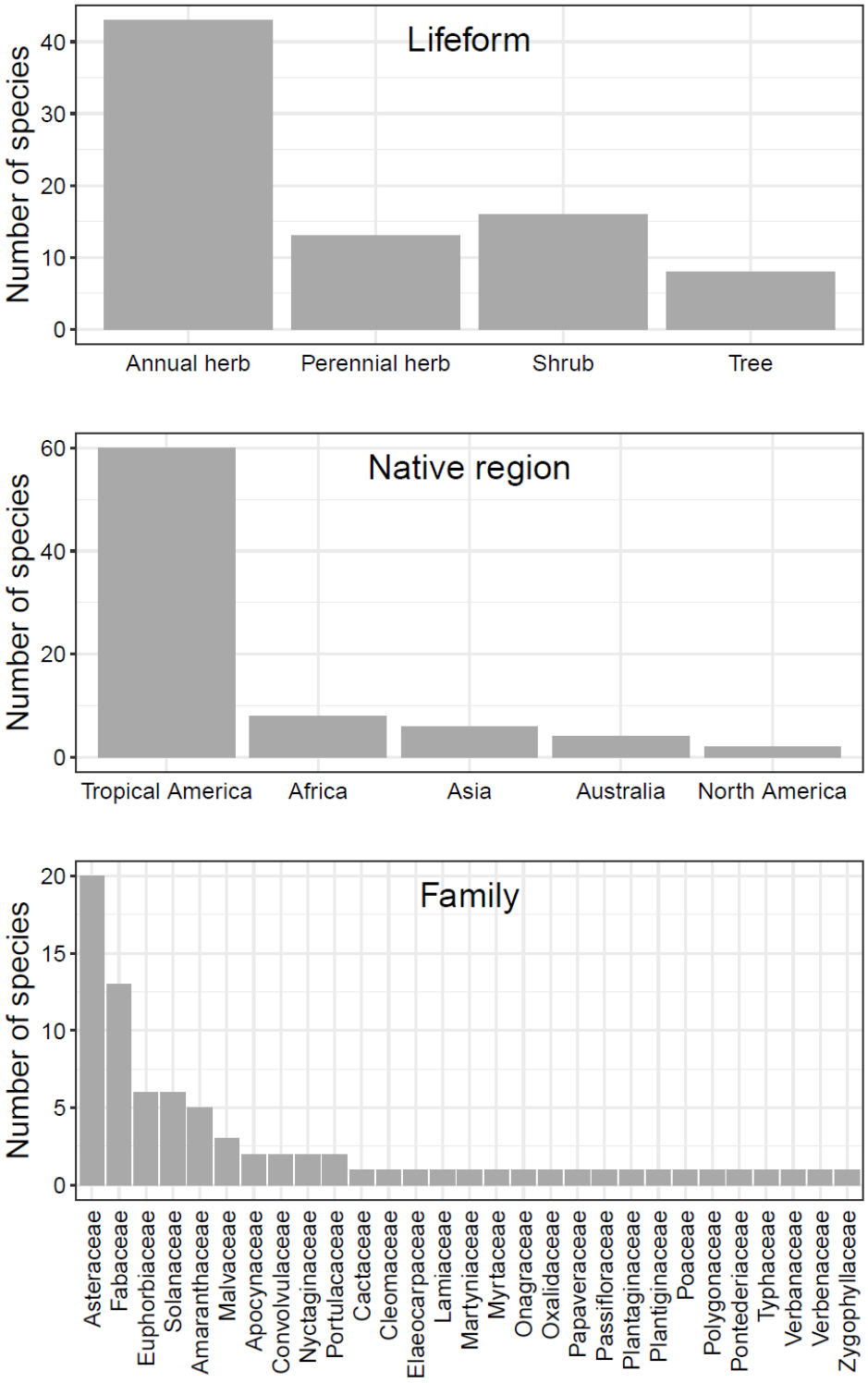
10) Name of species which were once invasive but are not anymore

Appendix 8: Invasive species of NWGK along with their first date of report from the region and range size (number of grids occupied)

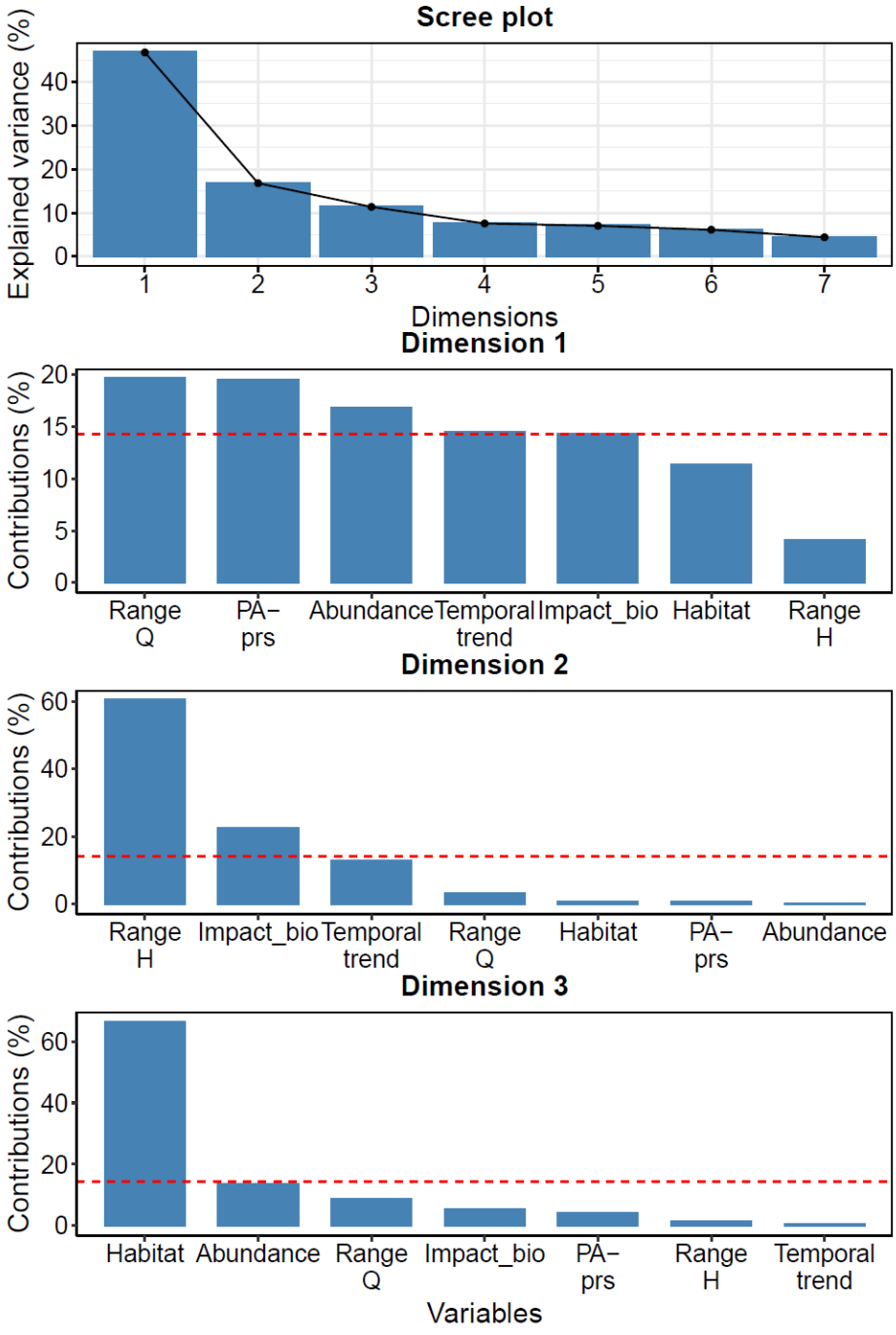
Species	First date of report	Grids occupied	Expert Rank
Acacia auriculiformis	1917	22	6
Acanthospermum hispidum	1945	46	8
Aeschynomene americana	1989	12	10
Ageratina adenophora	1917	10	8
Ageratum conyzoides	1839	92	7
Ageratum houstonianum	1950	6	
Alternanthera ficoidea	1839	11	3
Alternanthera paronychioides	1957	4	
Alternanthera pungens	1942	11	13
Alternanthera sessilis	1839	89	4
Antigonon leptopus	1893	8	
Argemone mexicana	1884	92	11
Asclepias curassavica	1839	29	12
Bidens biternata	1944	31	8
Bidens pilosa	1839	25	6
Boerhavia erecta	1966	6	
Senna tora	1861	80	8
Celosia argentea	1839	93	7
Chamaesyce hirta	1839	65	11
Chloris barbata	1839	21	10
Chromolaena odorata	1861	26	1
Cleome viscosa	1893	65	9
Cosmos bipinnatus	1908	9	9
Croton bonplandianum	1983	10	14
Cryptostegia grandiflora	1839	19	13
Dalbergia melanoxylon	1908	5	
Datura innoxia	1955	19	13
Datura metel	1861	27	9
Datura stramonium	1916	7	
Eclipta prostrata	1839	77	13
Eucalyptus globulus	1898	13	
Euphorbia heterophylla	1902	15	7
Euphorbia indica	1839	34	7
Galinsoga parviflora	1950	12	10
Mesosphaerum suaveolens	1908	39	2
Indigofera linnaei	1908	11	
Ipomoea carnea	1957	28	5
Ipomoea hederifolia	1956	34	8
Jatropha curcas	1894	42	13
Lagascea mollis	1839	44	11
Lantana camara	1908	82	3
Leucaena leucocephala	1903	23	7

Species	First date of report	Grids occupied	Expert Rank
Ludwigia erecta	1996	2	
Malachra capitata	1839	47	11
Malvastrum coromandelianum	1917	18	12
Martynia annua	1839	43	13
Mecardonia procumbens	1962	8	
Mikania micrantha	1996	1	
Mimosa pudica	1861	37	5
Mirabilis jalapa	1839	18	13
Monochoria vaginalis	1861	30	14
Muntingia calabura	2002	4	
Opuntia elatior	1908	18	13
Oxalis corniculata	1839	50	9
Parthenium hysterophorus	1955	15	6
Passiflora foetida	1839	27	13
Physalis angulata	1839	55	12
Portulaca pilosa	1839	3	
Portulaca quadrifida	1839	9	
Prosopis juliflora	1957	4	
Ricinus communis	1905	47	11
Scoparia dulcis	1896	52	12
Senna alata	1861	6	
Senna occidentalis	1861	31	11
Senna spectabilis	1861	1	
Senna uniflora	1993	2	
Solanum americanum	1996	2	
Solanum torvum	1839	17	14
Stachytarpheta jamaicensis	1839	3	
Stylosanthes hamata	1958	5	
Synedrella nodiflora	1945	40	4
Synedrella vialis	1996	2	
Tithonia diversifolia	1971	9	
Tribulus terrestris	1861	27	13
Tridax procumbens	1903	70	10
Triumfetta rhomboidea	1891	98	6
Typha domingensis	1839	12	11
Xanthium strumarium	1861	45	5
Zinnia peruviana	1839	6	

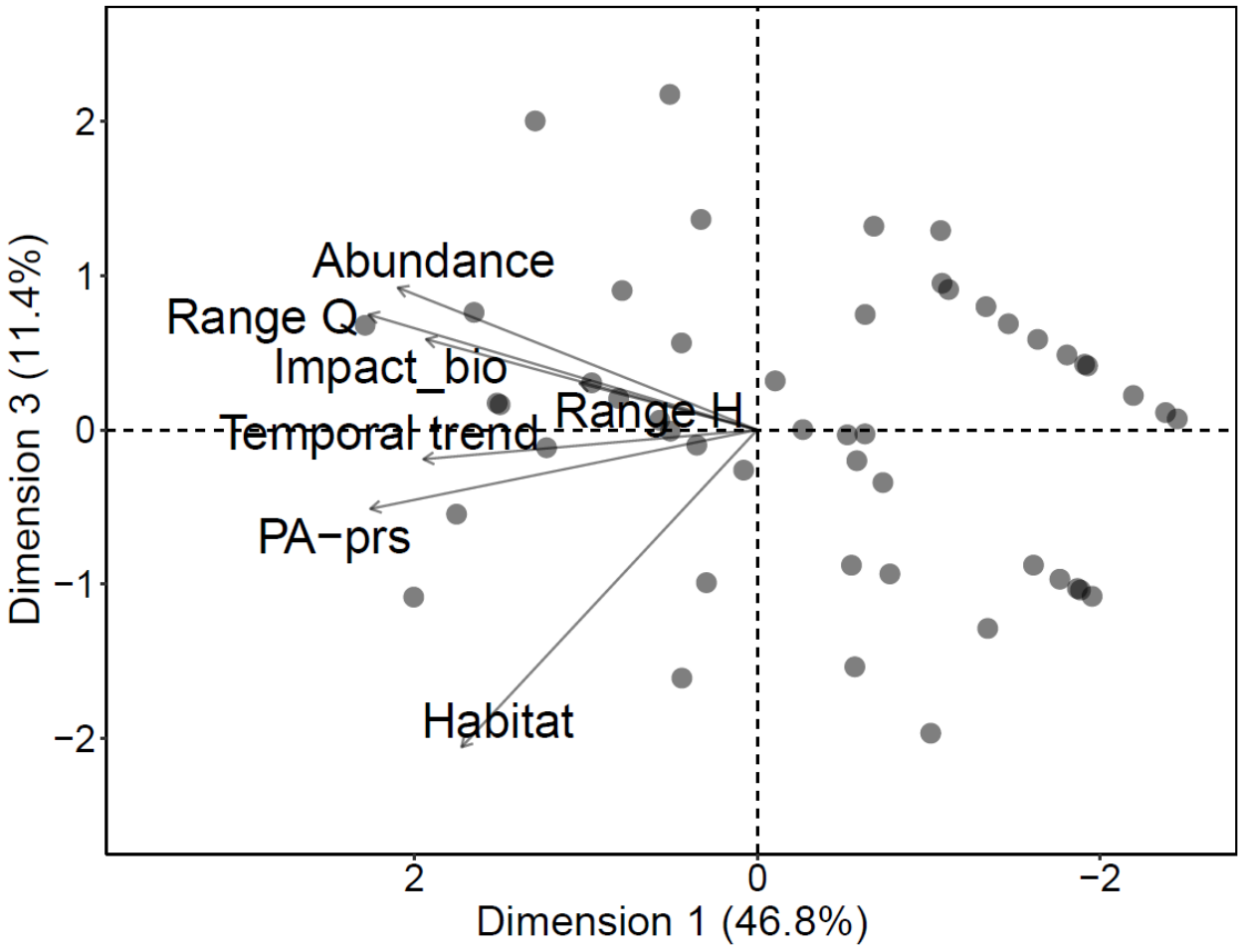
Appendix 9: Distribution of Lifeform, Native region and taxonomic family of the invasive plants of NWGK



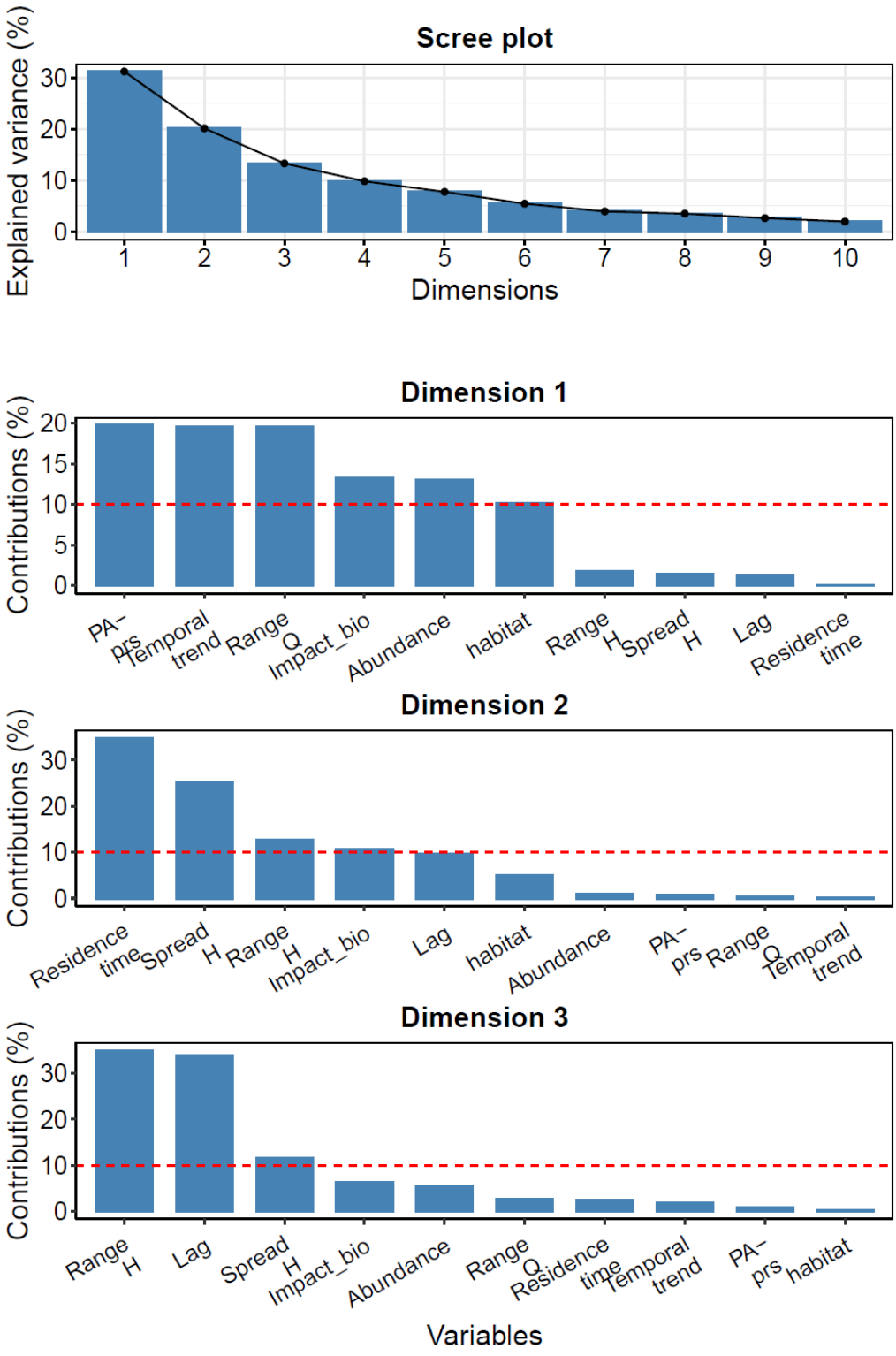
Appendix 10: Scree plots of PCA and loading on the first three dimension of PCA. PCA of ranks on different dimensions of invasion obtained through two complementary approaches. Range H- range size herbaria, Range Q- range size questionnaire, Habitat- habitat width, PA-prs- presence in protected areas, Abundance- local abundance, Impact_bio- impact on biodiversity.



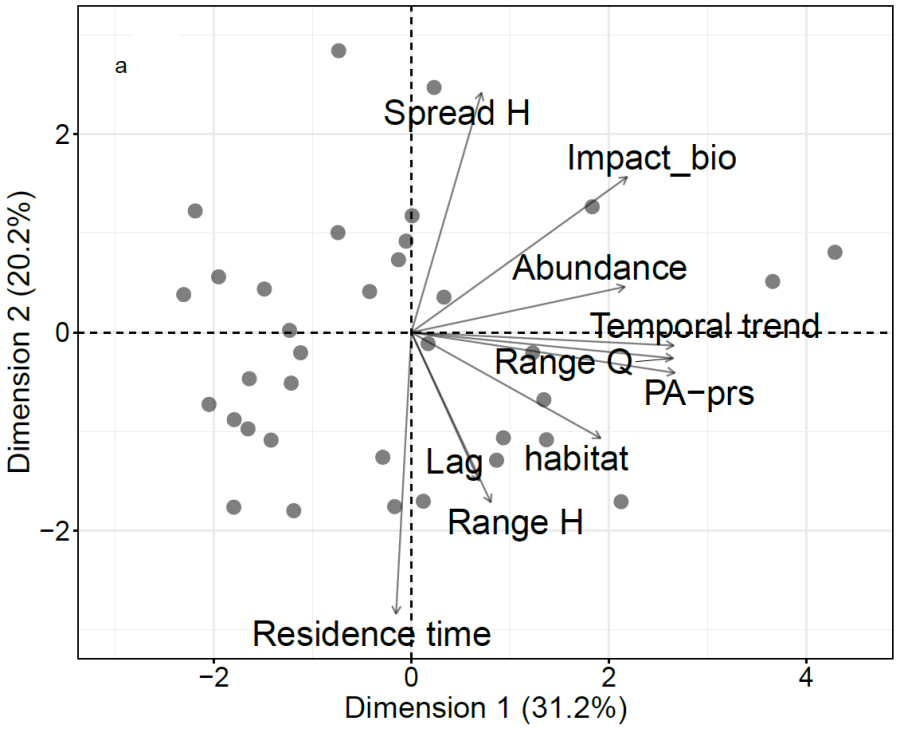
Appendix 11: Rank of species along the different dimensions of invasion obtained through two distinct complementary approaches i.e. herbaria and questionnaire. The graph shows the first and third dimension principal component. Range H- range size herbaria, Range Q- range size questionnaire, Habitat- habitat width, PA-prs- presence in protected areas, Abundance- local abundance, Impact_bio- impact on biodiversity.

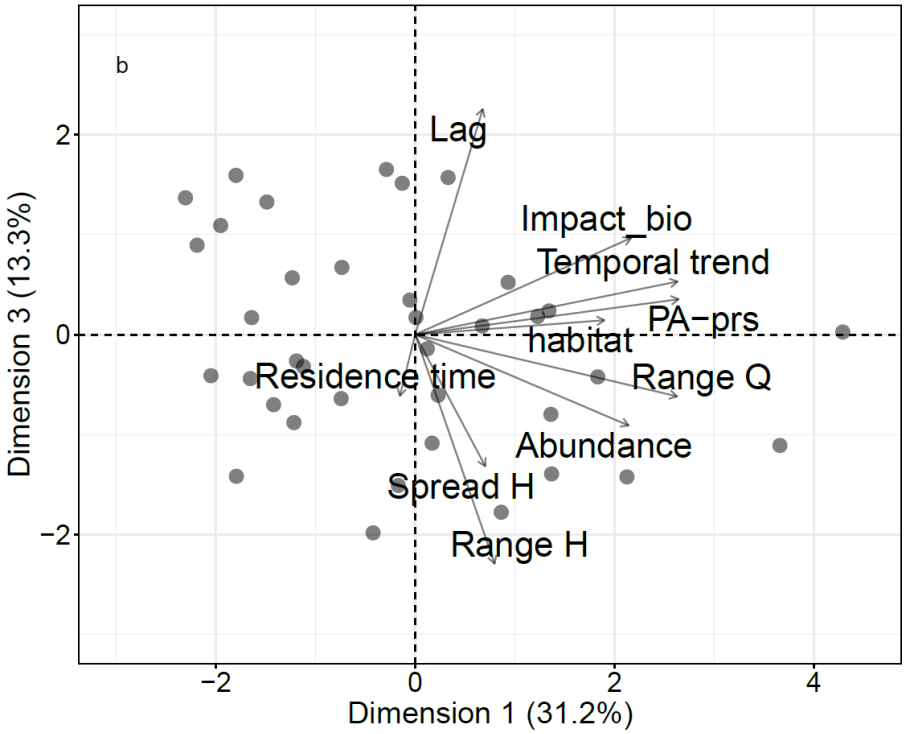


Appendix 12: Scree plots of PCA and loading of dimensions of invasion (including temporal dynamics from herbaria for 38 species) obtained through two distinct complementary approaches on the first three dimension of PCA.



Appendix 13: Rank of species along the different dimensions of invasion (including temporal dynamics from herbaria for 38 species) obtained through two distinct complementary approaches i.e. herbaria and questionnaire. a) First and second principal component; b) first and third principal component. Range H- range size herbaria, Range Q- range size questionnaire, Habitat- habitat width, PA-prs- presence in protected areas, Abundance- local abundance, Impact_bio- impact on biodiversity, Lag- lag phase.





Chapter 3: Functional trait distributions and ecological strategies of invasive plants of the Northern Western Ghats and Konkan regions

Introduction

Invasive plants use different strategies to acquire resources, reproduce and compete with co-occurring native species in a community. These strategies vary across environment and an optimal strategy helps a species grow, survive and reproduce under a given environmental condition (Baker 1965, Westoby et al. 2002) . The variability in these strategies can be captured by the functional traits of species, which are associated with species' function and performance (Díaz et al. 2016). Plant traits associated with distinct ecological strategies such as competition (height) and resource use (LMA) often determine the success of an invasive species (Pyšek and Richardson 2007). Studies have shown that invasive species have distinct and significantly higher values for performance related traits than the co-occurring native species (Van Kleunen et al. 2010).

Global study analyzing multi-trait distribution of over forty thousand plants has identified two major axis of variations in the plant performance and function. The first dimension associated with competitive and reproductive strategy of species is captured by traits such as height and seed mass. The second major dimension is associated with resource acquisition and is captured by traits such as leaf nitrogen and leaf mass per unit area (LMA) (Díaz et al. 2016). Studying functional traits of invaders can provide a comprehensive understanding of their ecological strategy (Küster et al. 2008). Traits are frequently associated with invasion success with invasive species often having higher competitive and faster resource use traits (Van Kleunen et al. 2010).

Comparing traits between invasive species and co-occurring native species can offer a mechanistic understanding of why certain invasions succeed (Carboni et al. 2016). For instance whether an invader will coexist or competitively exclude native species, can be predicted by assessing the degree of trait overlap between them. However, many of these studies quantify the difference across single trait and make an underlying assumption that single trait overlaps represent the niche overlaps (Sodhi et al. 2019). This need not always be the case, as differences along single trait axis are usually a reflection of competitive hierarchy (Funk and Wolf 2016). Therefore, to understand niche differences between invader and native it is crucial to study differences along multi-trait axis (Kraft et al. 2015). Studies have shown that multidimensional trait similarity between alien and native species can influence an invader's success. Non-native species can become invasive by two distinct mechanisms. They can either invade by niche expansion (being dissimilar to the native) (Divíšek et al. 2018) or by niche filling (occupying existing functional space as the native community) (Loiola et al. 2018). These contrasting results can be explained by invoking differential contribution of environmental filtering and biotic filtering in structuring the community. For instance, areas with stronger environmental filtering will allow, establishment of functionally similar invaders, but regions with higher biotic filter will permit only functionally dissimilar invasive species (Carboni et al. 2016).

Several ecological strategies schemes have been proposed to assess plant's performance and function. One of the most frequently studied and widely used is the CSR plant ecological strategy scheme. Variation in intensity of stress and disturbance determines the vegetation type and CSR strategies of plant communities in an area. Regions with high disturbance support species with ruderal strategies (R), whereas stress tolerant species (S) have better performance in

areas with high stress. Competitive species (C) have higher abundances in areas with low levels of disturbance and stress (Grime 1974). The C, S and R strategy of plants are associated with a set of vegetative and reproductive traits such as seed output, height etc. These traits help species to grow and reproduce under different levels of stress and disturbance (Grime 1974). Recent developments in the understanding of association between functional traits and ecological strategies has led to development of methodologies to quantify the competitive ability, ruderal strategy and stress tolerant capability of a species, using three leaf functional traits (Pierce et al. 2017). This method allows for global comparison of CSR strategies across various ecosystems and lifeforms (Pierce et al. 2017). Studies have shown that globally invasive species have high competitive and ruderal ability (Guo et al. 2019). Additionally, studies comparing CSR strategies of invaders with co-occurring natives have found evidences for both similarities (Fratte et al. 2019) and dissimilarities (Hasigerili et al. 2023) between them.

Invasive species are commonly linked to higher levels of disturbances, and the effect of these disturbances on their abundance tends to be greater in non-native regions compared to native region (Hierro et al. 2006). Additionally studies have shown close correspondence between CSR strategies of invaders with invasion success. For instance, as per expectation disturbance tolerant ruderal species have higher naturalization potential. However, interestingly it is not the ruderal habit but the competitive ability of a species which helps it become more widespread (Guo et al. 2019;Guo et al. 2022). Higher probability of naturalization of disturbance tolerant invaders can be a function of their trait syndrome. Ruderal species have traits, such as high flowering frequency and larger seed output, both of which make them desirable for introductions to new areas. Although these global studies provide interesting insights, these relationships can often

decouple at smaller spatial scales under different environmental conditions (Hasigerili et al. 2023).

In this chapter, I use a trait based approach to study invasive species of the Northern Western Ghats and Konkan regions (NWGK). Traits related to plant function and performance were measured and used to determine the CSR strategy of the species. I studied the distribution of traits of the invasive plant in this region to identify trait combinations associated with invasive species. Furthermore, to determine whether invasive species colonizes a region through niche filling or niche expansion, I compared trait space occupied by invasive species to that of co-occurring native species. Invader and co-occurring natives were also compared along the CSR ecological strategy space. Finally, to understand if certain trait combinations or ecological strategies are associated with successful invasion, relationship between different dimensions of invasiveness and traits/CSR scores of invasive plants in NWGK was quantified.

Methods

Trait quantification

I measured height, leaf traits: leaf area (LA), Leaf fresh weight (LFW), Leaf dry weight (LDW) and seed mass for five leaves and five individuals of the 78 invasive plants of the Northern-Western Ghats and Konkan regions (Harguindeguy et al. 2013). To measure the leaf traits, fresh weight, dry weight and leaf area for five leaves of each individual was estimated. Firstly, fresh weight of species was quantified followed by oven drying them at 80 degrees for 3 days, after which the dry weight was measured. Leaf dry matter content (LDMC) was quantified by dividing the fresh weight with the dry weight of the leaf. Leaf area (LA) was estimated by first

scanning fresh leaf using cannon lide 110 cam scanner followed by measuring the area using image j software. Dry weight divided by the total area measured was used to estimate the leaf mass per unit area (LMA). Mean trait value for each individual of each species was measured. Similar protocol was followed to quantify functional traits of native savanna species. Native species were selected from BLS based on their relative dominance, details of the selection are provided in chapter 5 of this thesis.

Distribution of species in trait space

To understand the multidimensional trait distribution of the 78 major invasive species, Principal Component Analysis (PCA) was performed using the factoextra package (Kassambara and Mundt 2020). All the traits were normalized by following suitable transformation prior to the analysis and I tested correlation between them (Appendix: Figure 1). To test if trait combination differs amongst invasive plants based on lifeform, a PERMANOVA was performed. Further, trait space of the native species (64 species) of the broad leaf savannas (BLS) with the co-occurring invasive species (21 species) were compared. To test if the trait space occupied by native species differs from the co-occurring invasive species I performed PERMANOVA using the vegan package (Oksanen et al. 2022).

Quantification of CSR strategy and distribution of species in CSR space

Leaf functional traits were used to quantify %C, %S and %R of each species following (Pierce et al. 2017). Similar protocol was followed to quantify the CSR strategy for the sixty four native species of Broad leaf savanna (BLS). Finally, CSR distribution of all the invasive species of NWGK and the invasive species of BLS with co-occurring native species was studied using the

ternary package (Smith and Sanselme 2024). To test if the CSR strategy of invasive differs from the co-occurring native species, firstly CSR scores were transformed using isometric log ratio (ILR) transformation. This aids in lowering the dimensions of the data, making it appropriate for multivariate analysis. I then used multivariate analysis of variance (MANOVA) using origin (native vs invasive) as independent variable and ILR transformed CSR scores as dependent variable.

Relationship between trait/CSR strategies with invasion success

To test the relationship between trait combinations of species with invasion success, an additive GLM was performed with PC scores as explanatory variable and number of grids occupied by the species as response variable. In a separate GLM, relationship was tested between individual traits with range size was also studied. To test the relationship between competitive, ruderal and stress scores with invasion success, a generalized linear model was used. In this model, %C, %S and %R were the explanatory variables and range sizes were the response variable. Additionally, to control for the effect of residence time on range size, residual from the best fit regression model between grids occupied and time since introduction was used as an explanatory variable in all the GLMs mentioned above. Other parameters of invasion success such as local abundance, habitat breadth and spread rate in region were also used as explanatory variables.

Results

Distribution of species in trait space

The principal component analysis was performed to understand the distribution of traits of the major invasive plants of NWGK. The first two principal component axes explained 72% of the

total variation (Figure 1; Appendix Figure 2). There are two major axis of variation, the first was associated with resource acquisition (LMA, LDMC) and another with competitive ability (LA, Height and Seed mass). Height which is associated with competition had a higher loading on PC1 axis, whereas traits related to resource acquisition (LMA and LDMC) had higher loading on the PC2 axis (Appendix: Figure 2). Invasive plants clustered differentially based on their life forms ($p < 0.001$), woody plants were taller and had higher LDMC and LMA than non-woody species. Invasive plants of savannas occupy a different trait space when compared with the native plant community ($p < 0.001$). The difference was along the PC 2 axis, with native species cluster having higher LDMC than the invasive species cluster (Figure 2a). However, this difference was being driven by differences in life forms. Native communities had many woody species, whereas invasive species were predominately herbaceous in nature. When only herbaceous native and invasive species were studied, the communities differ along the PC 1 axis. Invasive species had higher values for traits associated with competitive ability (leaf area and height) than native species (Figure 2b).

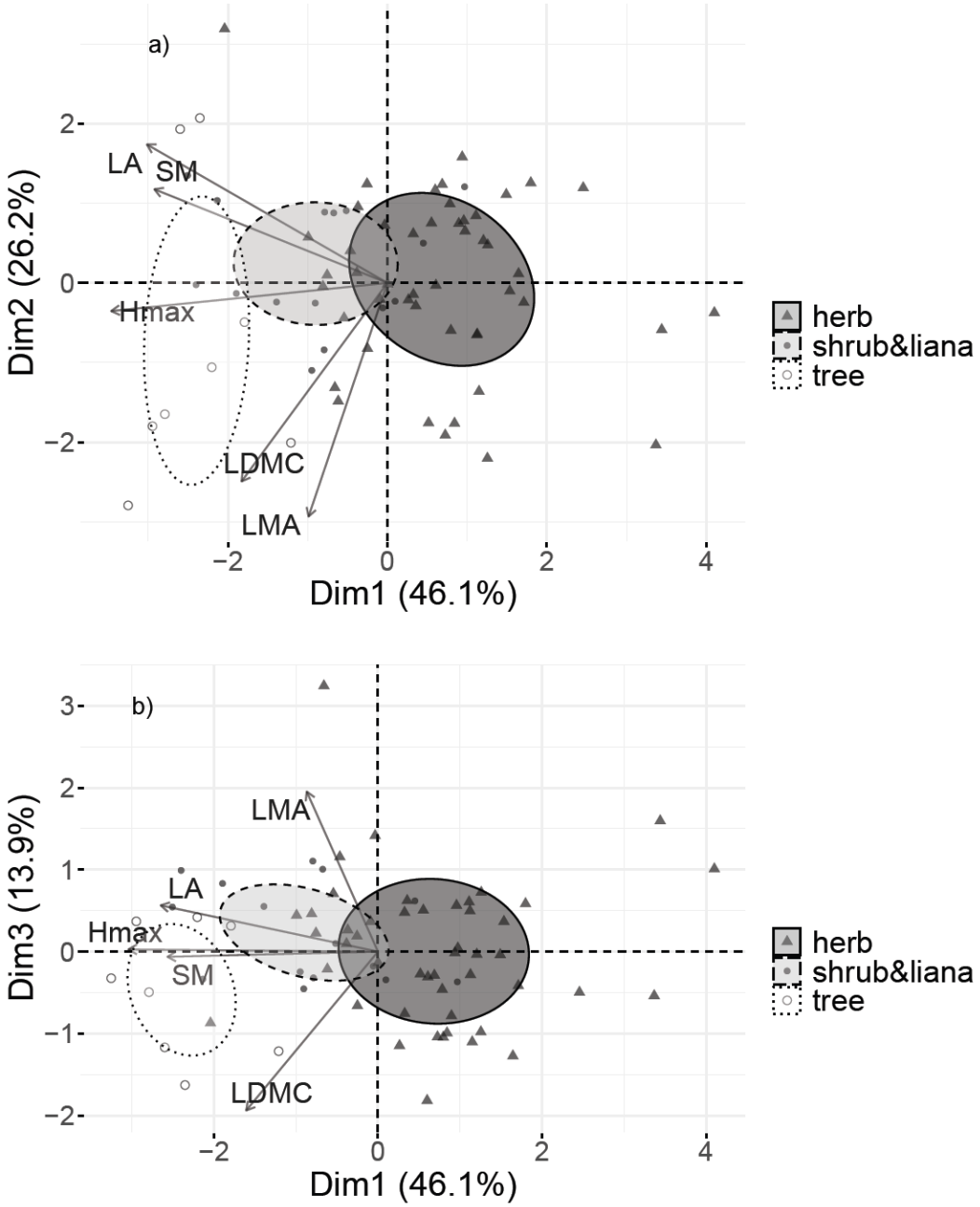


Figure 1: Distribution of traits of invasive plants of the Northern Western Ghats and Konkan regions (NWGK). PCA of five traits associated with competition (LA, H_{max}), resource use (LMA, LDMC) and reproduction (SM). a) The first two PC axis shown here, explains 72% of the total variation. b) Figure showing the first and third PC axis. Size and direction of vectors associated with traits represent the loading of the trait on the respective axis. The dark gray triangles represent herbaceous invaders, light gray solid circles are invasive shrubs and lianas and white hollow circles represent tree invaders of NWGK. Ellipses are 95% SE. LMA: leaf mass per unit area, LDMC: leaf dry matter content, H_{max}: maximum height, LA: leaf area and SM: seed mass.

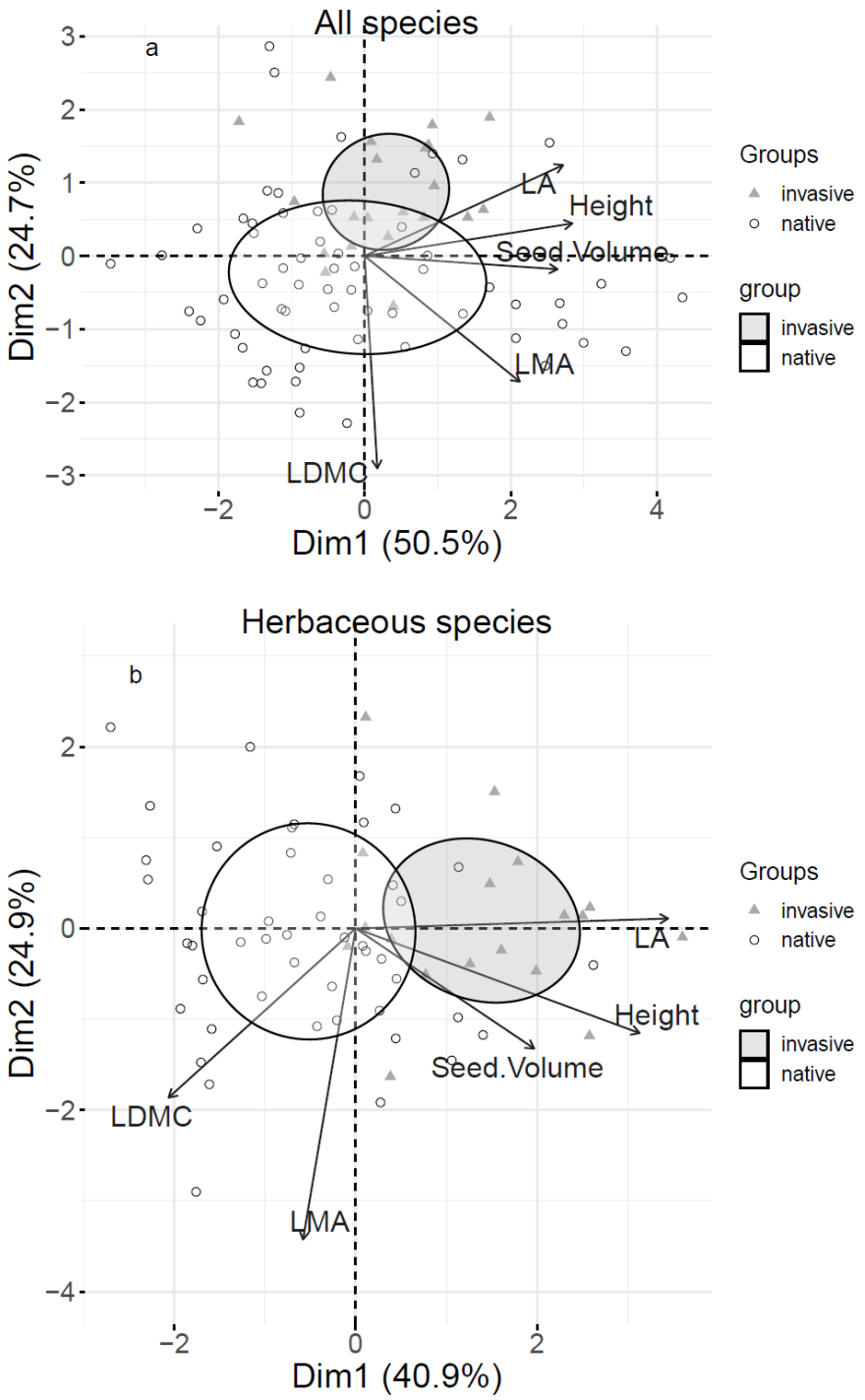


Figure 2: Trait distribution of invasive and native species of Broad leaf savannas (BLS). PCA of five traits associated with competition (LA, height), resource acquisition (LMA, LDMC) and reproduction (Seed volume) for a) both woody and non-woody species and b) herbaceous species only. Gray ellipse represent the invasive species and white ellipse represent the native species. Ellipses are 95% SE. LMA: leaf mass per unit area, LDMC: leaf dry matter content, LA: leaf area.

Distribution of species in CSR strategy space

Invasive species had moderate to high %C and %R scores. Overall they had very low to moderate %S scores (Figure 3). No species were found in the apex of the triangle avoiding specialized CSR strategies. When CSR strategy of invader was compared to the co-occurring native, I found that invaders occupy distinct CSR strategy space ($p < 0.001$). Native species clustered in the region of moderate to high ruderal and stress strategy and had low competitive ability, whereas invasive species had moderate to high ruderal and competitive scores and low stress scores (Figure 4).

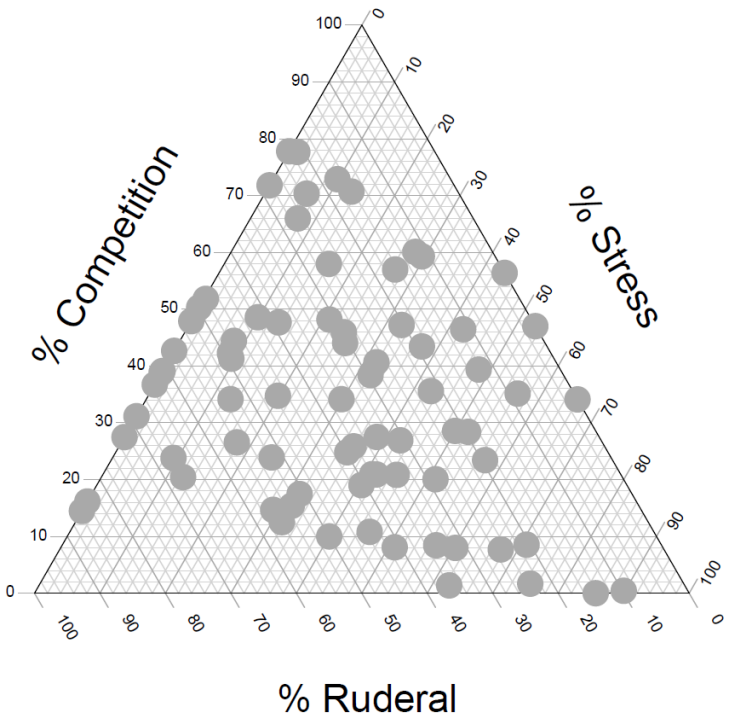


Figure 3: CSR strategy of invasive plants of the Northern Western Ghats and Konkan regions (NWGK). Ternary plot of the CSR strategy with axes of plot associated with competitive (C), Stress (S) or Ruderal (R) strategy. The gray points represent the invasive plants of NWGK.

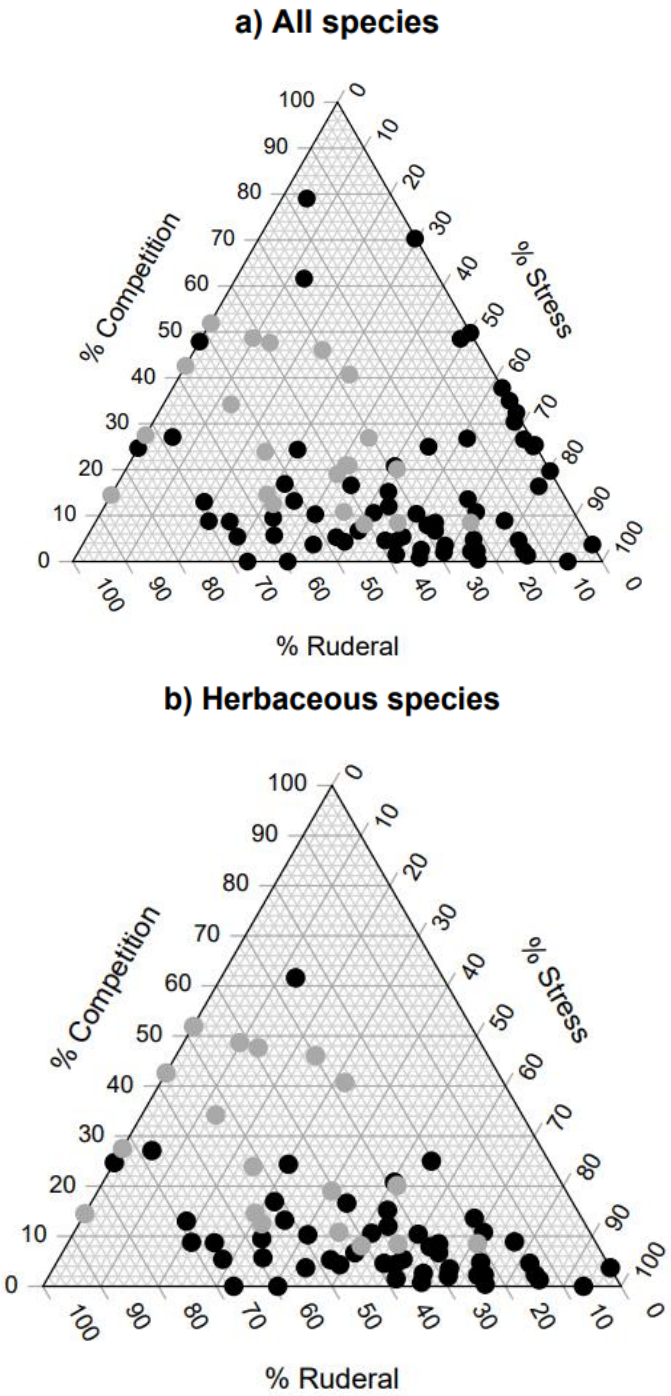


Figure 4: Distribution of invasive and native Broad leaf savannas (BLS) species in CSR strategy space. Ternary plot of the CSR strategy of a) both woody and herbaceous species and b) only herbaceous species. Axes of the ternary plot is associated with competitive (C), Stress (S) or Ruderal (R) strategy. The black points represent the native and gray points represent the invasive plants of NWGK.

Relationship between trait/CSR strategies with invasion success

When evaluating the relationship between species trait combination with range size, I also found a marginal relationship ($p < 0.1$) between the second PC axis with range size of species. Additionally, PC 1 was related to habitat breadth by species (Appendix: Table1). Univariate, only LDMC was marginally associated with growth rate of species ($p<0.1$). Results did not change when species' range sizes were controlled for their residence time (Appendix: Table1). Furthermore, ruderal score was positively ($p <0.05$) and stress tolerant was negatively ($p <0.05$) related with the species range sizes. No significant relationship was found between competitive ability and range size (Appendix: Table 2).

Discussion

In this chapter, I set out to understand the trait distribution of the major Invasive plant species in the Northern-Western Ghats and Konkan regions (NWGK). I found that variations amongst the invasive plants in this region can be explained along the competitive and resource use axis. Furthermore, I found that invader occupies a distinct trait space from the co-occurring native species. Similar differences were also found in the CSR strategies of invader and native species. Native species were more ruderal and stress tolerant whereas invaders were more competitive and ruderal. Furthermore, I found that the range sizes of an invader in NWGK are correlated with its ruderal habit and resource acquisitive traits.

Invasive plants of NWGK have two distinct axis of variation, the first being associated with resource acquisition and the other one related to competition. Woody invasive plants had traits corresponding to conservative resource use and were taller than the herbaceous invasive species.

Study has shown that majority of variation around global flora can be captured along the two major axis related to completion and resource use, where woody and non-woody species differ along the competitive axis (Díaz et al. 2016). This can be explained by the law of limiting similarity which states that invasive species which are functionally distinct from native community end up becoming more successful (Abrams 1983). Furthermore, I showed that invasive species found in savannas occupy a distinct trait space from the native species. Invaders were more resource acquisitive than native. However this difference was driven by differences in predominant lifeforms in these two categories. Native community had many woody species, whereas invasive species are predominantly herbaceous. Woody species are known to have higher LMA and LDMC than herbaceous species (An et al. 2021). For herbaceous species, native and invaders, differed along the competitive axis. Studies have shown that across different ecosystems invasive species differ from co-occurring natives along traits associated with resource acquisition and competition (Mathakutha et al. 2019; Díaz et al. 2021) but such differences are often contingent on lifeforms (Tecco et al. 2010). Interestingly, we did not find any difference along the reproductive axis between the invasive and native species of BLS.

Invasive species in NWGK avoid extreme C S or R values and have predominantly C, R and intermediate CSR strategy (Alexander et al. 2016). CSR strategies are mutually exclusive, and therefore invaders which are often generalists with wider climatic tolerance are expected to have intermediate C, S and R value. Such CSR combinations help them perform under disturbed, competitive and stressed conditions (Liu et al. 2017, Pierce et al. 2017). The Northern Western Ghats comprises of different types of habitats ranging from a competitive evergreen forests to

moderately to ruderal grasslands (Gadgil et al. 2011). Therefore it is not surprising that invasive plants in NWGK had a more generalist CSR score.

Ecological strategies, of invaders differed from that of the co-occurring native species. Invaders were more ruderal and competitive whereas native species are were more ruderal and stress tolerant. At regional scales invaders (Lambdon et al. 2008), or in habitats where environmental filter is stronger both invasive and native species have similar CSR strategy (Fratte et al. 2019), however in habitats with stronger biotic filter, invaders can follow the 'try harder' hypothesis and have different CSR strategy than natives (Dainese and Bragazza 2012). Studies from savannas have shown that successful invaders are often ruderal and are competitively superior to the native savanna species (Barbosa et al. 2015; Taylor et al. 2018).

Various traits and their combinations enable invasive species to invade different habitat types in NWGK, but certain trait combinations are more successful than others. Invaders possessing traits linked to higher Leaf Mass per Area (LMA) and Leaf Dry Matter Content (LDMC) have larger geographical ranges. Fast-growing invasive species that efficiently capture carbon and have shorter lifespans exhibit greater success, regardless of differences in reproductive output or competitive ability. These findings align with prior research indicating that the extent of invasion correlates with the invader's capability to utilize resources (Carboni et al., 2016). Additionally, contrary to global trend (Guo et al. 2019), I found that species with ruderal strategy had higher geographical range. The natural areas of NWGK are fragmented due to significant anthropogenic disturbances (Gadgil et al., 2011), which may facilitate the expansion of ruderal species that thrive in disturbed habitats (Grime, 1974).

Conclusion

Invasive plants of NWGK use different trait combinations to grow, reproduce and survive. However species with ruderal strategy have larger geographical extent in this region. This can be explained by high disturbance in this region which would facilitate the establishment of ruderals in this region. Increasing levels of disturbances in future can further exacerbate the problem of invasion in this region. In savannas surrounding the Western Ghats, invasive plants occupy a unique trait niche separate from native species, aligning with the law of limiting similarity. This distinction can inform strategies for screening and managing invasions in these savannas.

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Appendix

Tables

Figures

Figure 1: Spearman's correlation matrix between all functional traits. LA- Leaf area, SLA- Specific leaf area, (1/LMA), LDMC-leaf dry matter content, H_{max}- Height, SM- Seed mass. All the significant relationships are highlighted (Red- negative correlation; green- positive relationship)

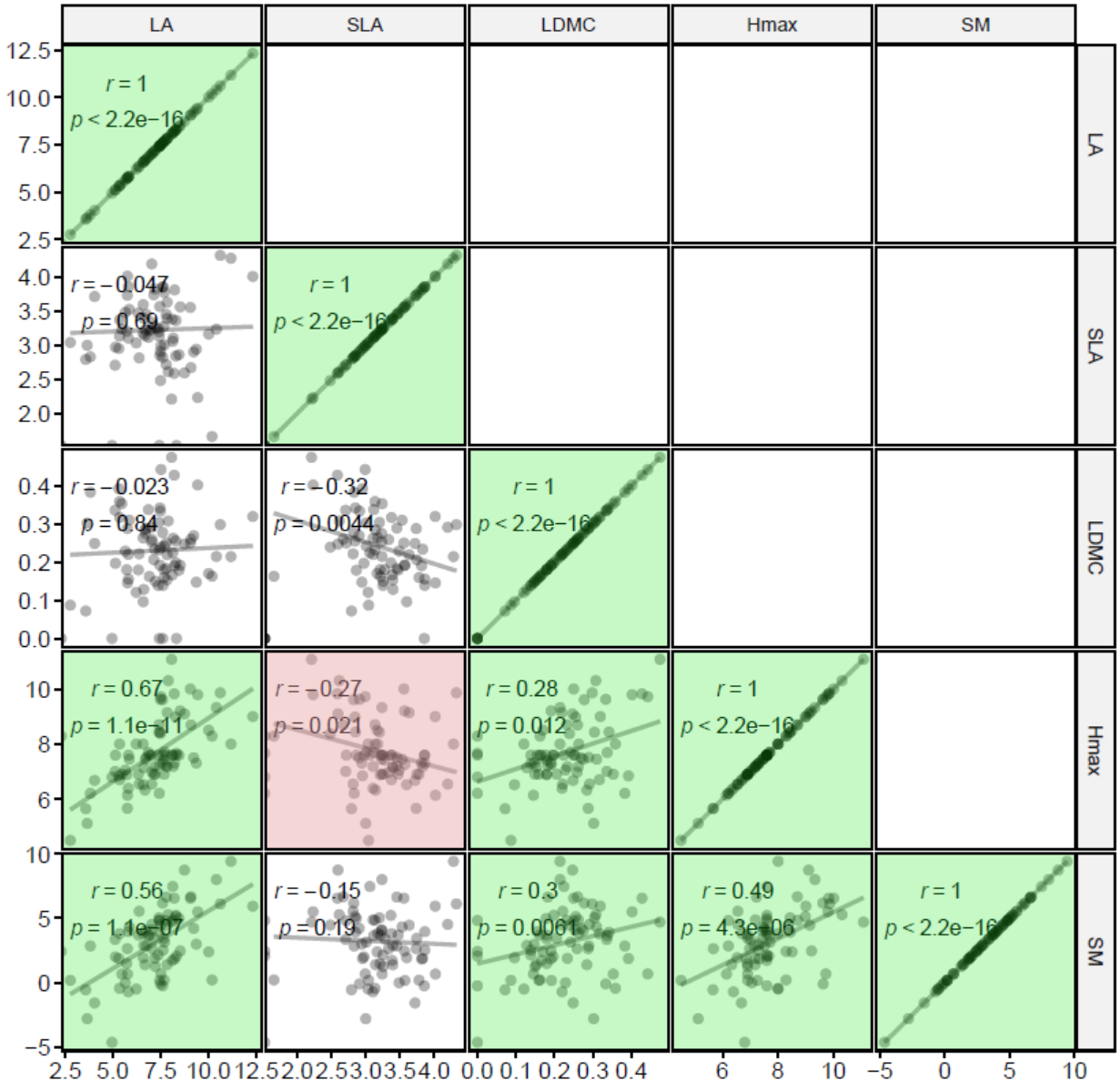


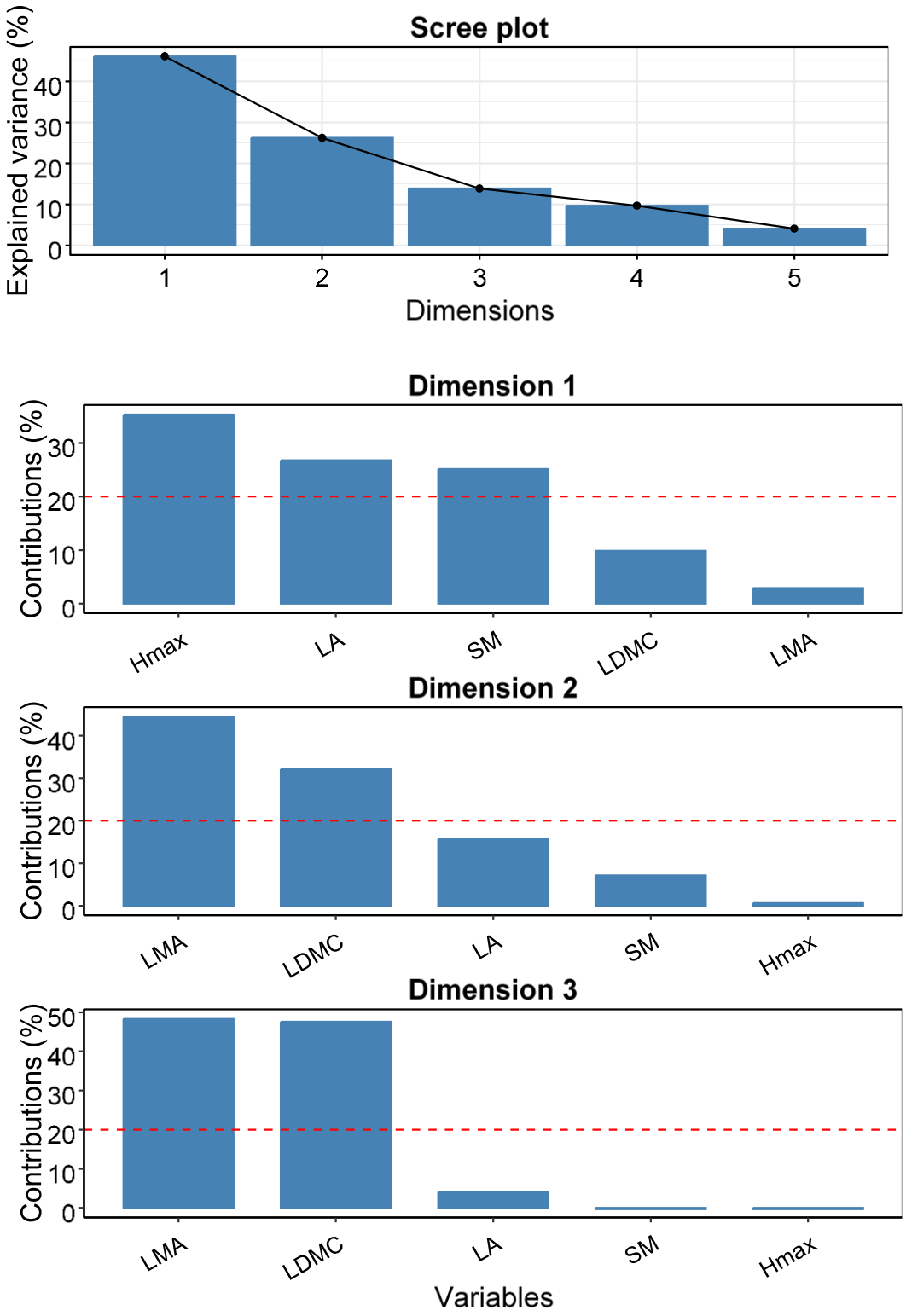
Table 1: Relationship of functional traits and PC axis with various aspects of invasion. GLM results show the relationship between traits and PC score of species with range size, range size controlled for residence time, spread rate, local abundance and habitat breadth. The signs represent the direction of relationship. Non-significant ($p>0.1$) relations have been marked as ns; marginally significant ($p<0.1$) have been marked as MS.

Individual traits	Range size	Range size (controlled for residence time)	Spread rate	Local abundance	Habitat breadth
H_{max}	ns	ns	ns	ns	ns
LA	ns	ns	ns	ns	-
SM	ns	ns	ns	ns	ns
LMA	ns	ns	ns	ns	ns
LDMC	ns	ns	+	ns	ns
pc1	ns	ns	ns	ns	+
pc2	(+)MS	(+)MS	ns	ns	ns
pc3	ns	ns	ns	ns	ns

Table 2: Relationship of CSR scores with various aspects of invasion. GLM results show the relationship between CSR score of species with range size, range size controlled for residence time, spread rate, local abundance and habitat breadth. The signs represent the direction of relationship. Non-significant ($p > 0.1$) relations have been marked as ns.

CSR strategy	Range size	Range size (controlled for residence time)	Spread rate	Local abundance	Habitat breadth
C	ns	ns	ns	ns	-
S	-	-	ns	ns	ns
R	+	+	ns	ns	+

Figure 2: Scree plots of PCA and loading of traits on the first three dimension of PCA. PCA of functional traits of invasive plants of NWGK.



Chapter 4: Differential impact of invasion on plant communities of two functional types of savannas in India

[This chapter has been submitted in its current form for communication to Ecological Applications, April 2, 2024]

ABSTRACT

Increasing biological invasions pose a threat to the high biodiversity in tropical savannas. Invasive plants can alter savanna communities in complex ways, and impacts can vary with the intensity of invasion and the spatial scales examined, and are likely modulated by climate. However, our understanding of such impacts on Asian tropical savannas is limited. To address this knowledge gap, we examined how invasion affected plant communities across increasing levels of invasion, at different spatial scales, in two climatically-determined savannas in tropical India. We sampled vegetation at three sites each in drier fine-leaf savannas (FLS), and wetter broadleaf savannas (BLS). At each site, we sampled replicate locations with plots assigned to uninvaded savannas, invaded savannas at three invasion levels, and remnant savannas that served as a benchmark for comparison. We quantified alpha and beta diversity, and differences in community composition that were partitioned into components representative of species loss and replacement. We found that while richness and diversity decreased linearly, evenness increased linearly with invasion. The loss of species was much greater in BLS (60 %) than in FLS (30 %). Changes in composition with invasion were more pronounced in BLS, and driven by species turnover in both savannas. Surprisingly, we did not find evidence of homogenization, with no difference in beta diversity in FLS, and an increase in BLS with invasion. These results highlight the utility of examining multiple measures of diversity, and show how differential effects on evenness can modulate how changes in richness translate to diversity. The linear responses with

increasing invasion suggest that management efforts may be equally effective at different stages of invasion in these savannas. Further, the observed increase in beta diversity in invaded BLS communities add to the growing reports of spatial scale dependent effects, and reinforce the need to examine invasion at multiple spatial scales. Overall, the greater loss of species and pronounced community changes in BLS which is the dominant savanna type in the Indian subcontinent and home to many endemic species suggests that it should be prioritized for conservation, management and future restoration.

INTRODUCTION

Invasive plant species have widespread effects on native communities across global biomes, including loss of diversity and altered composition (Hejda, Pyšek, and Jarošík 2009; Vilà et al. 2011). Among these biomes are tropical grasslands and savannas (hereafter savannas), which cover 20% of the earth's terrestrial surface, house high biodiversity, and provide a variety of important ecosystem services, including carbon sequestration and forage production (Dass et al. 2018; Parr et al. 2014). Tropical savannas span large climatic gradients, and invasive species cause significant reduction in native savanna biodiversity across the climatic gradients occupied by savannas (Foxcroft et al. 2010). Given the importance of tropical savannas for conserving global biodiversity and the widespread nature of invasion in this biome, halting the ongoing global biodiversity crisis will entail gaining a better understanding of the impact of biological invasions on tropical savannas (Chong et al. 2021). To that end, understanding how varying levels of invasion affect different measures of biodiversity at multiple spatial scales, and in savannas with diverse climates will help to conserve and restore global savannas.

Invasive plants affect communities in multiple ways, and the adverse impacts of invasions (Vilà et al. 2011), including on savannas, are well recognized (Foxcroft et al. 2010). For example, invasion resulted in a large reduction in species richness and diversity, and dramatic changes in community composition and structure in the Brazilian savannas (de Abreu and Durigan 2011). However, these effects are not universal, and the direction and strength of impacts often vary (Vilà et al. 2011). While invasion reduces both richness and diversity, the magnitude of change in richness is typically more pronounced than in diversity (Scasta et al. 2015). The impact of invasion on evenness is less well understood; while most studies report decreased evenness,

many show no change and a few report an increase in evenness with invasion (Powell, Chase, and Knight 2011). Understanding changes in evenness may help explain why effects of invasion on diversity are less pronounced than on richness (Hejda et al. 2021). It is also important to determine how invasion alters community composition (Seabloom et al., 2013) as such changes can be independent of changes in richness and diversity (Hillebrand et al., 2018). Further, partitioning changes in composition into components of nestedness and turnover allows us to determine the relative importance of species replacement versus loss (Andrés Baselga 2010). Overall, understanding the impact on diversity and composition allows the identification of species and lifeforms at risk, which can help managers make informed decisions for the conservation and management of savannas (Gooden et al. 2009).

The direction and magnitude of diversity loss with invasion at smaller scales does not always translate to similar changes at larger spatial scales (Powell, Chase, and Knight 2011). For instance, large impacts at local scales within communities may not be reflected at larger spatial scales if the effect of invasion differs across communities and results in greater heterogeneity across communities (Mason and French 2008). Although many studies, including of grassland communities report increased homogenization with invasion (Rolls et al. 2023), recent studies have shown that invasion can result in increased heterogeneity at larger scales (Stotz et al. 2017). Quantifying beta diversity and partitioning it into nestedness and turnover allows us to examine diversity at larger scales and determine the relative importance of species loss and species replacement (Campagnaro et al. 2018).

Native plant communities are exposed to varying abundances of invasive plants, and the impacts across different abundances will typically differ (Bradley et al. 2019). Studies that examine the impact of invasive species in the presence and absence of invader only, implicitly assume a linear abundance-impact relationship (Parker et al. 1999). Understanding whether the abundance-impact relationship is linear or curvilinear can provide important insight into underlying mechanisms. For example, density-dependent competitive interactions between invasive and native species are expected to result in non-linear impacts (Bradley et al. 2019). Additionally, the shape and strength of abundance-impact relationships have important implications for management decisions (Sofaer, Jarnevich, and Pearse 2018). With linear effects, management efforts may be equally effective at different stages of invasion, while for non-linear (convex) effects, interventions at early stages, when invader abundance is low, may be more effective (Sofaer, Jarnevich, and Pearse 2018; Yokomizo et al. 2009). Studies from European grasslands have found that abundance-impact relationships can be non-linear, and the nature of this relationship depended on invader identity, study area, plant groups examined, and the type of impact assessed (Fenesi et al. 2023). With the exception of temperate grasslands and a few Neotropical savannas (Siebert 2011), there are limited studies examining how invasive species affect native biodiversity across varying levels of invasion (Ratnam et al. 2016).

Savannas in tropical India are an important system to understand how biological invasions impact biodiversity given their large spatial extent, the presence of endemic flora, and the ecosystem services they provide (Nerlekar, Chorghe, et al. 2022; Ratnam et al. 2016). In addition to the direct loss of these savannas due to land use change (Madhusudan and Vanak 2023), anthropogenic pressures have resulted in the degradation remaining savannas, and spread of

invasive species in the remaining savannas (Sundaram & Hiremath, 2012). This may change for the worse as savannas are predicted to be the most vulnerable to future invasion compared to other ecosystems in tropical India (Mungi, Qureshi, and Jhala 2023). Invasion in tropical savannas in this region is associated with large reductions in native diversity (Sundaram & Hiremath, 2012), and studies have shown that removal of invasive species can help successfully restore native biodiversity (Nerlekar, Mehta, et al. 2022).

In this study, we examined the effects of invasive plants in two savanna types in tropical India that differ in mean annual precipitation: wetter broadleaf savannas and drier fine-leaf savannas (Ratnam et al. 2016). Rainfall and water availability are important for determining the establishment and abundance of invasive plants (Seabloom et al. 2013), and modulating interactions between invasive plants and co-occurring native species (Esch et al. 2018). Therefore, we might expect that the impacts of invasion would differ between wetter BLS and drier FLS. Specifically, we asked how: 1) species richness, evenness and diversity differs across an invasion gradient at local scales? 2) How species composition shifts with increasing invasion, and how species replacement versus species loss influences such composition shifts? And, 3) How invasion alters diversity at larger spatial scales? We sampled three sites in broadleaf savannas and fine-leaf savannas in western Maharashtra, India across three levels of invasion. In addition to the invasion gradient, we sampled uninvaded and old-growth plant communities to compare and contextualize our findings. We hope that the results of this study will shed light on the threats of invasion and help to formulate strategies to manage invasion in savannas.

METHODS

Selection of site: There are two types of savannas in peninsular India: the broadleaf savannas (BLS) characterized by a mean annual precipitation (MAP) of 700-2100 mm; and the fine-leaf savannas (FLS) with MAP of 400-1000 mm. This study was carried out in Western Maharashtra, India, which has both FLS and BLS. Potential sites were identified for FLS with MAP < 600 mm, and BLS with MAP > 800 mm based on previous studies that describe savannas in this region (Dabadghao and Shankarnarayan 1973; Nerlekar et al. 2024). Three sites in each savanna type were finally selected after preliminary surveys based on the presence of invasion species (Appendix: Figure S1, S2; Table S1). In BLS sampling was done in Pune, Dandoba and Khambatki and sampling sites in FLS were Laling, Saswad and Mograle. Invasive species were defined as species which are not native to the Indian subcontinent and are known to have negative impacts on biodiversity.

The broadleaf savannas typically have relatively higher tree densities, and common trees include *Anogeissus latifolia*, Combretaceae; *Terminalia tomentosa*, Combretaceae; and, *Lannea coromandelica*, Anacardiaceae. Common grasses (Poaceae) include *Themeda* spp, *Heteropogon contortus* and *Lophopogon tridentatus* (Dabadghao and Shankarnarayan 1973). The major invaders in BLS in this region are woody shrubs (e.g., *Lantana camara*, Verbanaceae; *Mesosphaerum suaveolens*, Lamiaceae) and semi-woody shrubs (e.g., *Chromolaena odorata*, Asteraceae). Tropical savannas in general, and BLS in particular have a high number of the endemic plant species, many of which have only recently been described (Nerlekar, Chorghe, et al. 2022; Singh et al. 2015).

The fine-leaf savannas have sparse tree cover and the same common grasses that occur in BLS. In contrast to BLS, the major invaders in FLS are herbaceous species that include *Parthenium hysterophorus*, Asteraceae; and *Senna uniflora*, Fabaceae. Woody invasive species like *Lantana camara* and *Mesosphaerum suaveolens* occasionally co-occur with herbaceous invaders but at much lower abundances (Appendix: Table S2).

Field Sampling: Sampling was done in the peak growing season (August-October) of 2021 and 2022. Five locations which were a minimum of 300 m from each other, were identified at each site. At each location, we sampled five 100m^2 (10 m × 10 m) plots that were assigned to one of five categories: remnant, uninvaded, low invasion, medium invasion, and high invasion. The level of invasion was determined by visual estimation of the percent cover of invaded species: uninvaded (~ 0%), low (~30%), medium (~50%), and high (>80%) (Appendix: Figure S3). Uninvaded plots allowed a comparison between invaded communities and the native savanna communities. However, some of the uninvaded plots were in secondary savannas (i.e., post-agricultural), and old-growth savannas in these locations were present in areas that were topographically and edaphically different, making a strict comparison to invaded plots difficult. To provide a reference for how invasion changed community composition, we sampled remnant (old-growth) savannas at each location (Nerlekar et al. 2024). A total of 155 100m^2 plots were sampled: 5 plots (remnant, uninvaded, three invasion levels) × 5 locations (one site had six locations) × 3 sites × 2 savannas (Appendix: Figure S2, S3).

In each 100m^2 plot, we measured the cover of herbaceous species in ten 1 m^2 quadrats. These ten quadrats were spread out on three transects within the 100 m^2 plots. The first and the third

transects had three quadrats each, located at 3, 5 and 7 m from the edge of the plot, and the second transect had the remaining four quadrats at a distance of 2, 4, 6 and 8 m from the edge of the plot (Appendix: Figure S3). We visually estimated the percent cover of herbaceous species in each 1 m^2 quadrat. We estimated the dominance of trees with DBH ≥10 cm by quantifying GBH at 1.3 m for all individuals in the 100m^2 plots. When trees had multiple stems we measured the GBH of each stem. To measure percent cover of shrubs we used three transects placed in each 100m^2 plot at a distance of 2, 5 and 8m from the plot's edge. We summed the length of these transects intercepted by shrubs.

Data analysis: The total percentage cover for herbaceous species in each plot was estimated by taking the sum of cover for each species in the ten 1 m × 1 m quadrats. Species richness was quantified as the sum of the unique species for the ten quadrats in each plot. Similarly, Pielou's evenness and Shannon diversity were estimated using the cumulative richness and cover for all ten quadrats using the vegan package (Oksanen et al. 2022). We performed generalized linear mixed effect model (GLMM) analyses for alpha diversity (richness, evenness and diversity) as response variables. The categorical levels of invasion and the savanna types were included as interactive fixed effects, and site as a random effect. Since species richness is count data, we performed Poisson GLMM in the lme4 package (Bates et al. 2023). We used type III Wald chi-square tests on the GLMM model estimates using car package for test of significance (Fox et al. 2023). In addition to the above analyses, which examined the entire herbaceous community including invasive species, we also performed analyses for just the native herbaceous community. Separate GLMM analyses were used to examine differences between uninvaded and remnant plots. Finally, to test if presence of woody species in FLS has an effect on different

measures of alpha diversity a GLMM analysis was done with measures of alpha diversity (richness, evenness and diversity) as response variables. The categorical levels of invasion and invader's life form were included as interactive fixed effects, and site as a random effect.

To test the nature of the relationship between abundance of invasive species and biodiversity, we performed separate mixed effect models with linear and polynomial functions. Richness, evenness and diversity were included as response variables, invasive percent cover as a fixed effect, and site as a random effect. The dominant invaders in BLS are woody species, whereas in FLS, they are herbaceous species. Therefore, invasive cover estimates were for woody invaders in BLS, and herbaceous invaders in FLS (Appendix: Figure S4, S5). AIC scores were used to determine whether the linear or polynomial functions better described the impact of invasive species.

To examine differences in the composition of communities across the invasion gradient, we performed a non-metric multidimensional scaling (NMDS) analysis using the metaMDS function of Vegan (Oksanen et al. 2022). Species identity and abundance was used to calculate the pairwise bray dissimilarity. We used k = 3 dimensions and made sure that the stress value was leass than 0.2 (K. R. Clarke 1993). We used the first two NMDS axes to visualize difference in composition, and performed a permutational multivariate analysis of variance (PERMANOVA) using the adonis function in the vegan package to understand how invasion and savanna type contributed to the differences in composition. Additionally, the envfit function from the vegan package was used to identify species which were driving compositional differences, and to

determine the direction and strength of change in abundance of these species across the invasion gradient.

To estimate the direction and magnitude of differences in composition with increasing levels of invasion, we estimated abundance weighted dissimilarity (bray dissimilarity) between uninvaded plots and the different levels of invasion. The total bray dissimilarity was partitioned into nestedness and turnover. All of the above pairwise comparisons were made using the beta.pair function of the betapart package (Andres Baselga et al. 2023) . Finally, we performed GLMM analyses with compositional change parameter (bray dissimilarity, turnover, nestedness) as response variables, invasion level and savanna type as interactive fixed effects, and site as a random effect. We performed the type III Wald chi-square tests to assess the significance of each fixed effect. In addition to the above analyses, which examined the entire herbaceous community including the invasive species, we also estimated bray dissimilarity for the native herbaceous community. We performed supplementary analyses with incidence based dissimilarity (presence/absence of species), and compared incidence based and abundance based results for composition differences to identify if the differences are driven by dominant or rarer species (Mason and French 2008). To understand if the difference in composition between uninvaded plots and remnant plots differ in the two savannas, we performed welsh two sampled t-test because of unequal variances.

Finally, to understand if invaded communities become more homogeneous, we measured beta diversity at a larger spatial scale, i.e. for each site, and partitioned beta into nestedness and turnover (betapart package, Andres Baselga et al. 2023). Following this, a GLMM analysis was

performed with beta diversity (total beta, turnover, nestedness) as a response variable, invasion levels and savanna types as fixed effects, and site as a random effect. Type III Wald chi-square tests were performed to assess the significance. To understand if the beta diversity of our control plots differs from the old growth savanna, we ran a separate GLMM with uninvaded and remnant plots. In addition to the above analyses, which examined the entire herbaceous community including the invasive species, we also estimated total beta dissimilarity for just the native herbaceous community. In a supplementary analysis, we compared the incidence and abundance based beta diversity to determine if diversity at larger spatial scale is influenced by dominant or rare species (Mason and French 2008). All the analyses were performed in R version 4.1.1.

RESULTS

Total plant species richness declined across the invasion gradient (Figure 1a) in both savannas, but to a greater extent in broadleaf savannas (Table 1). On average, the number of species decreased from 24 to 8 (~66%) in BLS, and from 22 to 15 (~30%) in FLS. Evenness increased across the invasion gradient for both savanna types (Figure 1b; Table 1). Diversity also decreased across the invasion gradient, but the effect was less pronounced than with richness (Figure 1c; Table 1). There were no differences between remnant and uninvaded communities for richness, evenness or diversity (Appendix: Table S3). Comparing the above results which included the entire community including the invasive species with results for analyses with only the native species showed no differences for species richness (Appendix: Table S4). However, results for evenness and diversity changed when only the native communities were examined. For the native communities, evenness did not change with invasion, and FLS hade marginally higher evenness than BLS (Appendix: Table S4). For diversity, in addition to the main effect of

invasion that was also seen for the entire community, native communities for FLS had higher diversity than BLS (Appendix: Table S4). Linear declines were better than polynomial fits in explaining the change in richness, evenness, and diversity as a function of increasing invasion (Appendix: Table S5).

Composition in the two savannas were different and changed in distinct ways with increasing invasion (Figure 2a; Appendix: Table S6). In both FLS and BLS, increasing invasion led to the decline of some native grasses (e.g., *Chrysopogon fulvus, Melanocenchris jacquemontii, Heteropogon contortus*) and forbs (e.g., *Cyanotis fasciculata, Rostellularia procumbens*). This decline in native species was compensated in FLS by the increase in invasive forbs (e.g., *Parthenium hysterophorus, Senna uniflora, Triumfetta rhomboidea*), and some native grasses (e.g., *Apluda mutica, Themeda quadrivalvis* and *Urochloa ramosa*) (Appendix: Figure S6, S7; Table S7, S8).

Dissimilarity increased across the invasion gradient, but to a greater extent for BLS (~55%) than for FLS (~33%) (Figure 2b; Table 2). Both components of dissimilarity, turnover and nestedness increased with invasion for both savannas (Figure 2c, 2d; Table 2). The contribution of turnover was greater than nestedness, and this was particularly pronounced for FLS where approximately 75% of the dissimilarity was due to turnover. Unlike with abundance based measures of dissimilarity, both savannas showed similar increases in dissimilarity when incidence based composition differences were examined (Appendix: Table S9, S10; Figure S8). There were no differences in dissimilarity or its components between remnant and uninvaded communities

(Appendix: Table S11, S12). These results did not change when examining the composition of native communities without the invasive species (Appendix: Table S13).

To understand the impact of invasion at larger spatial scales, we examined how beta diversity for each site changed with invasion. Beta diversity increased with invasion for BLS, but did not change for FLS (Figure 3a, Table 3). Overall, turnover rather than nestedness contributed more to beta diversity. There was no change in turnover with increasing invasion for BLS, and a decrease for FLS (Figure 3b). On the other hand, nestedness increased across the invasion gradient in both savannas (Figure 3c). Unlike with the abundance based measure of beta diversity, incidence based measures of beta diversity were similar for both savannas (Appendix: Table S14; Figure S9). There were no significant differences between remnant and uninvaded plots in beta diversity or its components (Appendix: Table S15, S16). Both savannas showed increased beta diversity when only the native species in the community were examined (Appendix: Table S17).

DISCUSSION

In this study, we set out to understand the impact of invasion on composition and diversity of savanna communities at multiple spatial scales. We found a linear decline in species richness with increasing invasion, and this was more pronounced in broadleaf savannas (BLS) than in fine-leaf savannas (FLS). Communities across both savannas became more even, and less diverse with increasing invasion. Community composition changed across the invasion gradient with more prominent changes in BLS than in FLS. Overall, species replacement contributed more to

differences in composition than species loss. In examining the impacts of invasion at a larger spatial scale, we did not find any evidence for homogenization in these savanna communities. Contrary to expectations, highly invaded sites in BLS actually had higher beta diversity and were more heterogeneous than uninvaded communities.

Richness decreased in a linear manner with increasing invasion for both savannas, but the magnitude of the decrease was much greater in BLS. An importance difference between the two savannas is the prevalence of woody invaders in BLS. Woody species are likely to have larger adverse impacts on the native herbaceous communities (Pyšek et al. 2012), and this may explain the more pronounced impacts observed for BLS. However, when we tested whether woody invaders show greater impact in FLS, where both woody and herbaceous invaders were present, we found that woody invaders did not affect the magnitude of impact (Appendix: Table S18). In contrast to richness, invasion in both savannas resulted in similar linear increases in evenness. However, when only the native communities without the invaders were examined, evenness did not change with invasion. Thus, the increase in evenness in the overall community may result from multiple dominant invasive species with similar abundances. Invasive species can help other invaders establish themselves and can become co-dominant in a given area (Simberloff & Holle 1999). Additionally, the loss of rarer species because of strong competitive inhibition by dominant invaders may result in more equidistributional patterns of abundance and increased evenness (Routledge 1983). Predominantly, our results show that the impact of invasion changes linearly for both savannas, and for the different measures of diversity examined. These results support assumptions made in earlier studies (Parker et al. 1999), and are congruent with

empirical studies from various ecosystems, which show a linear abundance impact relationship (Bradley et al. 2019).

Similar to what has been shown in other grasslands we found that invasion drastically alters the composition of these savannas (Ahmad et al., 2019). Compositional differences can result from changes in both the identity and relative abundance of species (Andrés Baselga, 2016), and comparison of dissimilarity measures based on abundance weighted versus incidence based methods can help identify the importance of changes in species identity as opposed to relative abundance. While we did not find any difference in dissimilarity measured with and without abundance in BLS, we found that abundance weighted dissimilarity was lower than incidence based dissimilarity in FLS. This suggests that changes in composition in FLS were largely driven by rarer species. In both savannas invasion resulted in the decreased abundance of important species that serve as indicators of old growth savannas, e.g. *Chrysopogon fulvus, Melanocenchris jacquemontii* and *Cyanotis fasciculata* (Appendix S1: Figure S6, S7) (Nerlekar et al. 2024). Both species loss and species replacement increased with invasion in these savannas. Overall, species replacement contributed more than species loss to changes in community composition, and this suggests that empty niches created by species loss with invasion were being occupied efficiently by a new set of species (Ulrich, Almeida-Neto, and Gotelli 2009).

Invasion can differentially affect biodiversity at different spatial scales, and quantifying beta diversity helps connection local effects to regional and landscape level impacts (Powell, Chase, and Knight 2011). Invasion by a few common and widespread invasive species which dominate

the systems that they invade can result in biotic homogenization, and such homogenization and decreased beta diversity due to invasion has been widely reported, including in savannas (Kortz & Magurran, 2019). Contrary to this, we found no evidence of biotic homogenization in these and actually saw an increase in beta and heterogeneity in BLS communities. In BLS, the increase in beta was consistent when comparing both abundance and incidence based measures of dissimilarity. However, in FLS, the increased heterogeneity of invaded systems was only observed with incidence based dissimilarity measures, and there were no differences in heterogeneity the when species abundances were taken into consideration. This suggests that in FLS changes in presence of rare species is driving the observed increase in heterogeneity, whereas in BLS higher heterogeneity results from changes in species presence and abundance.

Our results show that invasion can result in large reductions in plant diversity in Asian tropical savannas, similar to what is known from other parts of the world (Vilà et al. 2011). The impact of invasion was consistently higher in broadleaf savannas for multiple measures of biodiversity. This is alarming as BLS form the largest fraction of Indian savannas (Ratnam et al. 2016) and harbor higher percentages of endemic species (Nerlekar, Chorghe, et al. 2022). Given limited resources, we recommend that BLS should be prioritized for management against invasive species. Additionally, we found that increased evenness of invaded communities may explain why decreases in diversity were not as strong as decreases in richness (Xu et al. 2022). Based on different conservation objectives, different measures of diversity may be more important for assessing impacts (Hurlbert 1971). For instance, richness indices may suffice when the primary goal is to preserve species, but Shannon diversity might be a more relevant for site restoration efforts, where both species numbers and proportional abundances matter (Nerlekar, Mehta, et al.

2022). Invasive species are replacing several native savanna species, leading to changes in the composition of these savannas. Many of the native savanna species identified in this study as vulnerable to invasion are indicator species of old growth savannas, and should be preserved as a priority (Nerlekar et al. 2024).

Contrary to expectations, at larger spatial scales invaded areas in these savannas were more heterogeneous. This suggests that focusing conservation and management efforts across multiple locations may be more important than focusing on single larger areas in one location(Latzka et al. 2016). Finally, the linear impacts of invasion observed in these savannas suggests that management efforts may be equally effective at different stages of invasion (Simberloff 2003). Thus, early management efforts like maintaining natural regimes of fire and herbivory (Foxcroft et al. 2010) can be effective, but interventions at advanced stages like removal of invasive species and controlled burning can also be helpful (Thekaekara et al. 2017).

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AUTHOR CONTRIBUTIONS

Conceptualization: MO, DB; methodology: MO, ANN, DB; data collection: MO, BKS, DB, ANN, MND, BC; analysis: MO, DB; data curation, MO; writing: MO, ANN, DB; funding acquisition: MO, DB.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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Table 1: Change in alpha diversity across the invasion gradient in broadleaf savannas and fine-leaf savannas. Diversity measures include: a) richness; b) evenness; and, c) Shannon's diversity. The results presented are for type III Wald chi-square for diversity measures with savanna and invasion gradient as fixed effects, and site as a random effect.

Response	**Effects**	**X^2**	***df***	***p* value**
a) Richness	Intercept	12.441	1	4.20E-04
	Savanna	4.161	1	0.041
	Invasion gradient	113.014	3	2.20E-16
	Savanna × Invasion gradient	13.798	3	0.003
b) Evenness	Intercept	201.231	1	2.20E-16
	Savanna	0.624	1	0.429
	Invasion gradient	14.331	3	0.002
	Savanna × Invasion gradient	5.949	3	0.114
c) Shannon diversity	Intercept	46.777	1	7.96E-12
	Savanna	2.109	1	0.146
	Invasion gradient	6.311	3	0.097
	Savanna × Invasion gradient	0.177	3	0.981

Table 2: Shifts in composition across the invasion gradient for broadleaf savannas and fine-leaf savannas. a) Shift in composition measured as bray dissimilarity (abundance weighted); and partitioned into: b) turnover; and, c) nestedness to understand species replacement and species loss, respectively. Results presented are for a type III Wald chi-square test for composition dissimilarity and its components with savanna type and Invasion gradient as fixed effects and site as a random effect.

Response	**Effects**	$\mathbf{X^2}$	***df***	***p* value**
a) Dissimilarity	Intercept	83.912	1	2.20E-16
	Savanna	16.478	1	4.92E-05
	Invasion gradient	62.821	2	2.28E-14
	Savanna × Invasion gradient	8.346	2	0.015
b) Turnover	Intercept	17.980	1	2.23E-05
	Savanna	12.008	1	0.001
	Invasion gradient	10.538	2	0.005
	Savanna × Invasion gradient	0.822	2	0.663
c) Nestedness	Intercept	6.541	1	0.011
	Savanna	1.556	1	0.212
	Invasion gradient	11.802	2	0.003
	Savanna × Invasion gradient	3.225	2	0.199

Table 3: Beta diversity for each site across the invasion gradient in broadleaf savannas and fine-leaf savannas. a) Abundance based beta diversity (bray beta diversity); and its components: b) turnover; and, c) nestedness. The results presented are for type III Wald chi-square for beta diversity and its components with savanna and Invasion gradient as fixed effects and site as a random effect.

Response	**Effects**	**X^2**	***df***	***p* value**
a) Beta diversity	Intercept	137.250	1	2.20E-16
	Savanna	1.276	1	0.259
	Invasion gradient	18.041	3	4.31E-04
	Savanna × Invasion gradient	15.597	3	0.001
b) Turnover	Intercept	52.852	1	3.60E-13
	Savanna	0.143	1	0.705
	Invasion gradient	1.573	3	0.666
	Savanna × Invasion gradient	12.969	3	0.005
c) Nestedness	Intercept	1.181	1	0.277
	Savanna	0.486	1	0.486
	Invasion gradient	8.985	3	0.030
	Savanna × Invasion gradient	0.945	3	0.815

Figure legends

Figure 1: Impact of increasing levels of invasion on alpha diversity estimated as: a) Species richness (species/10m^2); b) Evenness; and, c) Shannon diversity. Gray lines represent the fine-leaf savanna and black lines the broadleaf savanna. Rem - Remnant plots which represents old growth savannas; Un-I - uninvaded plots which had minimal invasion; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P -values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

Figure 2: a) Community composition (abundance-weighted) represented in non metric multidimensional scaling (NMDS) axis-1 and axis-2. The solid black line with the arrow were added as a visual aid to represent changes in BLS, and the gray line for FLS; ellipses represent 95% SE. b) Abundance weighted compositional differences (bray dissimilarity) between uninvaded and invaded plots; c) turnover; and, d) nestedness. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

Figure 3: Beta diversity for each site across invasion gradient in broadleaf savannas and fine-leaf savannas: a) Beta diversity (abundance weighted); b) turnover, c) nestedness. Gray lines represent the fine-leaf savanna and black lines the broadleaf savanna. Rem - Remnant plots which represents old growth savannas; Un-I - uninvaded plots with had minimal invasion; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive

species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

Figure 1

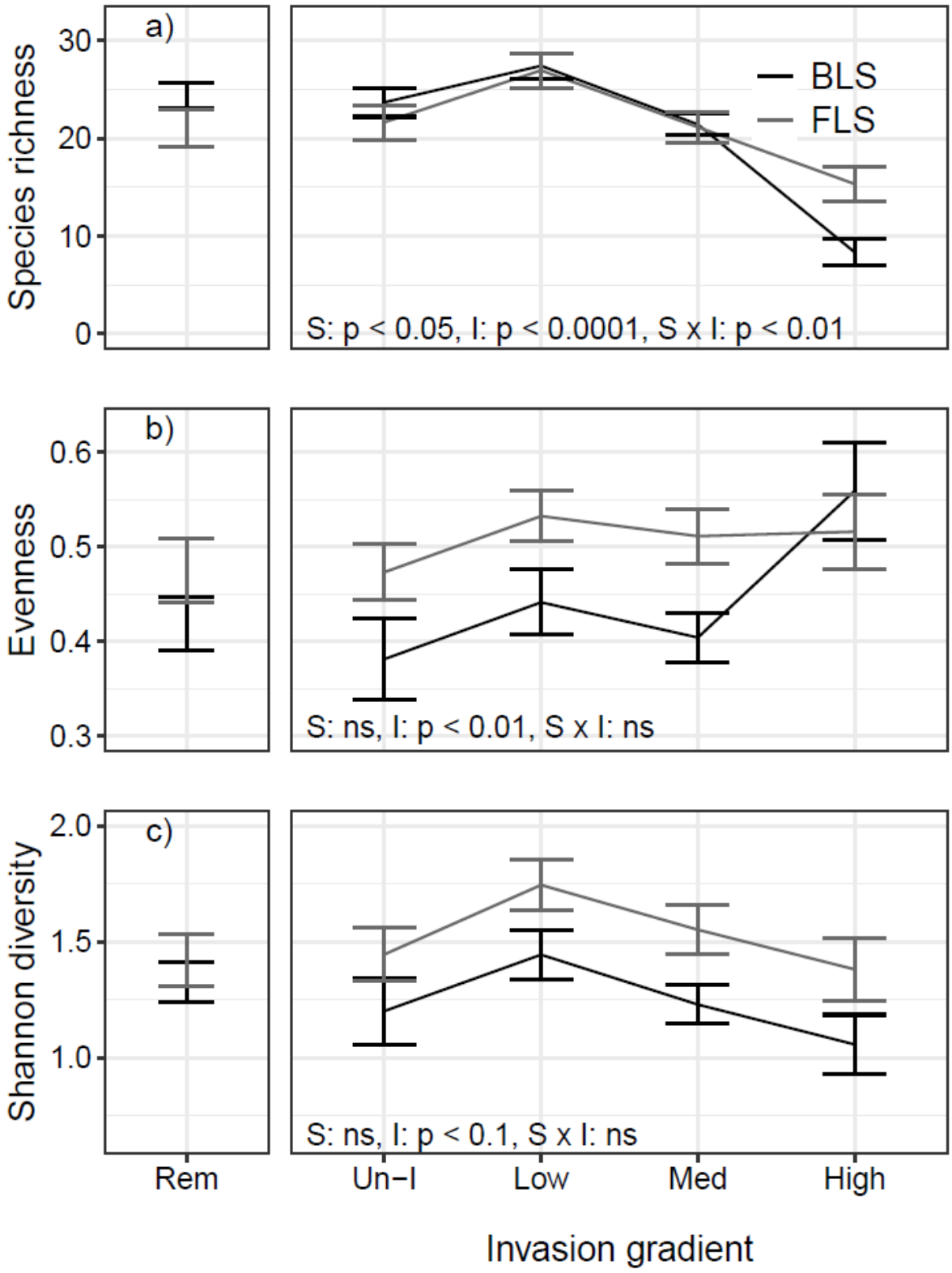

a)
Species richness
30
20
10
0
BLS
FLS
S: p < 0.05, I: p < 0.0001, S x I: p < 0.01
b)
Evenness
0.6
0.5
0.4
0.3
S: ns, I: p < 0.01, S x I: ns
c)
Shannon diversity
2.0
1.5
1.0
S: ns, I: p < 0.1, S x I: ns
Rem
Un−I
Low
Med
High
Invasion gradient

Figure 2

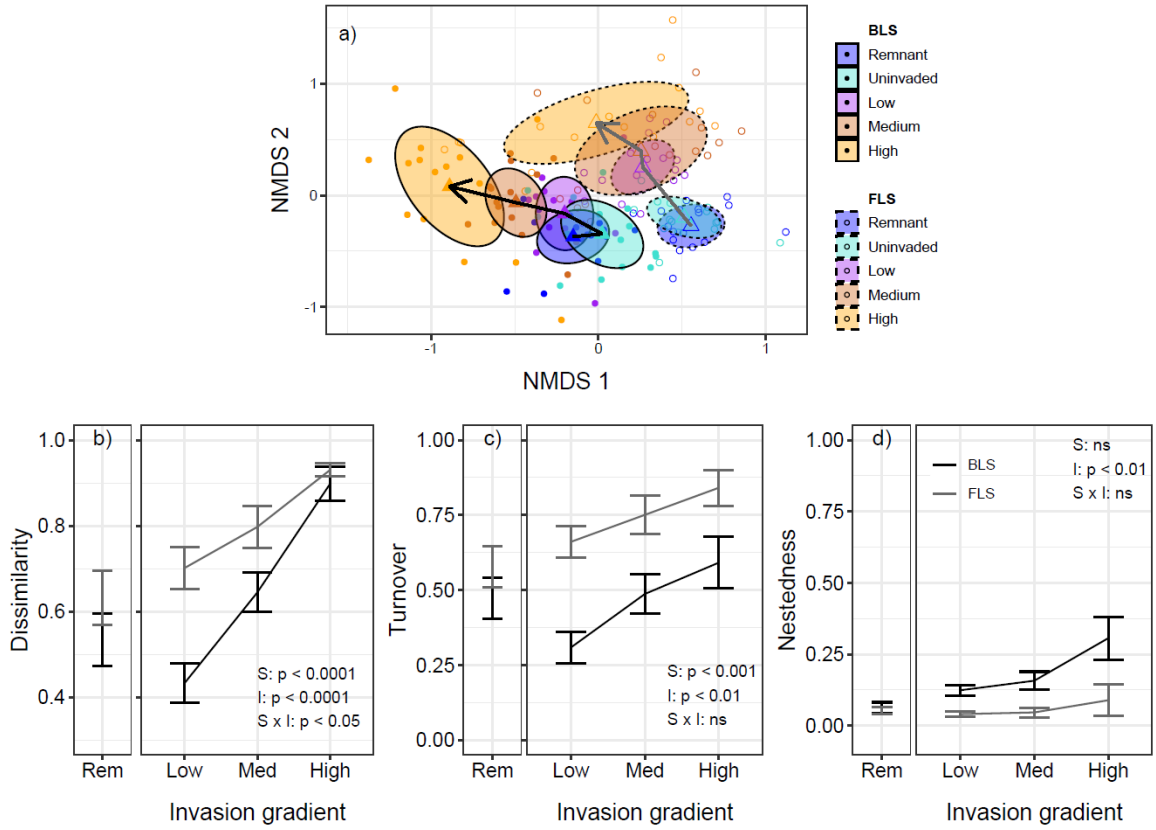
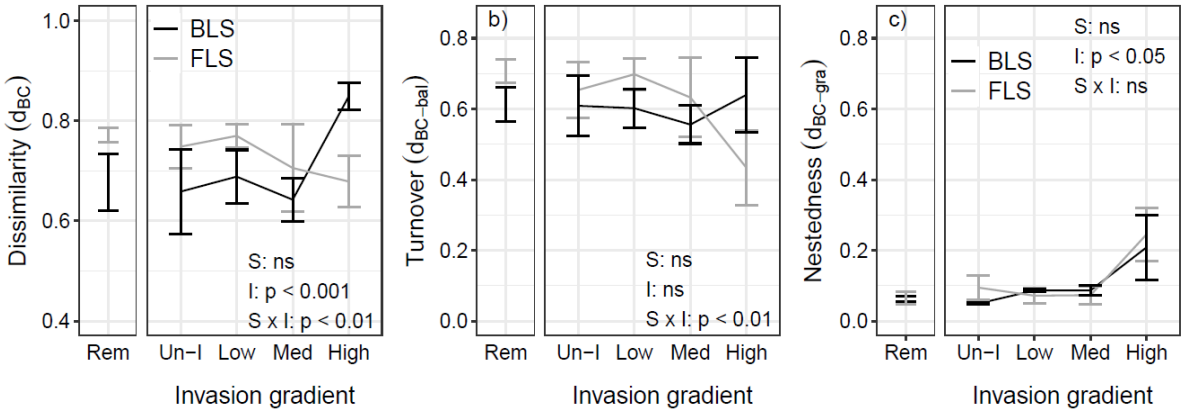


Figure 3



Ecological Applications

Appendix

Differential impact of invasion on plant communities of two types of savannas in India

M. Ojha, Bhushan K. Shigwan, Ashish N. Nerlekar, Mandar N. Datar, B. Chavan, D. Barua

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Table S17: Difference between entire community and native community in abundance based beta diversity and its components across invasion gradient in the two savannas.

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FIGURES

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Figure S2: Representative image of savanna sites.

Figure S3: Study design showing sites, locations, plots and quadrats.

Figure S4: Cover of all herbaceous invasive species in fine-leaf savanna.

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Figure S6: Direction of change in abundance of species of fine-leaf savanna in the NMDS ordination space.

Figure S7: Direction of change in abundance of species of broadleaf savanna in the NMDS ordination space.

Figure S8: Incidence based compositional dissimilarity (Sorenson) between uninvaded and invaded plots.

Figure S9: Incidence based beta diversity for each site across invasion gradient.

Table S1: GPS co-ordinates (decimal degrees) of 31 locations sampled across six sites in two savannas

Savanna	Site	Location	Latitude	Longitude
Broadleaf savanna	Dandoba	Dandoba 1	16.93822	74.75105
Broadleaf savanna	Dandoba	Dandoba 2	16.93855	74.75239
Broadleaf savanna	Dandoba	Dandoba 3	16.93693	74.74945
Broadleaf savanna	Dandoba	Dandoba 4	16.93272	74.75132
Broadleaf savanna	Dandoba	Dandoba 5	16.93939	74.74488
Broadleaf savanna	Khambatki	Khambatki 1	18.00668	74.01767
Broadleaf savanna	Khambatki	Khambatki 2	18.00746	74.01663
Broadleaf savanna	Khambatki	Khambatki 3	18.0068	74.01633
Broadleaf savanna	Khambatki	khambatki 4	18.00684	74.01613
Broadleaf savanna	Khambatki	khambatki 5	18.00764	74.01456
Broadleaf savanna	Pune	Bavdhan hill	18.53284	73.80493
Broadleaf savanna	Pune	Pune-sus 2	18.54863	73.78475
Broadleaf savanna	Pune	Pune-Sus hill	18.55013	73.78442
Broadleaf savanna	Pune	Pune-ARAI	18.52493	73.81663
Broadleaf savanna	Pune	Pune-Chaturshingi	18.53942	73.82665
Fine-leaf savanna	Laling	Laling 1	20.80492	74.73558
Fine-leaf savanna	Laling	Laling 2	20.84064	74.7585
Fine-leaf savanna	Laling	Laling 3	20.75601	74.92946
Fine-leaf savanna	Laling	Laling 4	20.66652	74.81361
Fine-leaf savanna	Laling	Laling 5	20.80437	74.72981
Fine-leaf savanna	Mograle	Mograle 1	17.86763	74.50515
Fine-leaf savanna	Mograle	Mograle 2	17.86845	74.50496
Fine-leaf savanna	Mograle	Mograle 3	17.9255	74.51584
Fine-leaf savanna	Mograle	Mograle 4	17.85742	74.52007
Fine-leaf savanna	Mograle	Mograle 5	17.89458	74.51165
Fine-leaf savanna	Saswad	Dh 1	18.43472	17.18471
Fine-leaf savanna	Saswad	Dh 2	18.42722	74.19535
Fine-leaf savanna	Saswad	Dh 3	18.43327	74.16733
Fine-leaf savanna	Saswad	Mn	18.41162	74.11414
Fine-leaf savanna	Saswad	Dh 5	18.40732	74.22288
Fine-leaf savanna	Saswad	Dh 6	18.28849	74.18106

Table S2: List of invasive species found in broadleaf savanna and fine-leaf savanna

Broadleaf savanna		**Fine-leaf savanna**	
Species	**Family**	**Species**	**Family**
Acanthospermum hispidum	Asteraceae	*Acanthospermum hispidum*	Asteraceae
Aeschynomene americana	Fabaceae	*Alternanthera sessilis*	Amaranthaceae
Alternanthera sessilis	Amaranthaceae	*Bidens pilosa*	Asteraceae
Bidens pilosa	Asteraceae	*Cassia auriculata*	Fabaceae
Celosia argentea	Amaranthaceae	*Celosia argentea*	Amaranthaceae
Chloris barbata	Poaceae	*Chloris barbata*	Poaceae
Chromolaena odorata	Asteraceae	*Cleome viscosa*	Cleomaceae
Euphorbia hirta	Euphorbiaceae	*Euphorbia heterophylla*	Euphorbiaceae
Lagascea mollis	Asteraceae	*Euphorbia hirta*	Euphorbiaceae
Lantana camara	Verbenaceae	*Euphorbia indica*	Euphorbiaceae
Mesosphaerum suaveolens	Lamiaceae	*Lagascea mollis*	Asteraceae
Oxalis corniculata	Oxalidaceae	*Lantana camara*	Verbenaceae
Parthenium hysterophorus	Asteraceae	*Leucaena leucocephala*	Fabaceae
Senna tora	Fabaceae	*Malvastrum*	Malvaceae
Senna uniflora	Fabaceae	*Mesosphaerum suaveolens*	Lamiaceae
Stylosanthes hamata	Fabaceae	*Parthenium hysterophorus*	Asteraceae
Synedrella nodiflora	Asteraceae	*Prosopis juliflora*	Fabaceae
Tecoma stans	Bignoniaceae	*Senna uniflora*	Fabaceae
Tridax procumbens	Asteraceae	*Synedrella nodiflora*	Asteraceae
Triumfetta rhomboidea	Malvaceae	*Tribulus terrestris*	Zygophyllaceae
Xanthium strumarium	Asteraceae	*Tridax procumbens*	Asteraceae
		Triumfetta rhomboidea	Malvaceae
		Vachellia planifrons	Fabaceae
		Xanthium strumarium	Asteraceae

Table S3: Differences between remnant and uninvaded plots for: a) richness; b) evenness; and, c) Shannon diversity. The results presented are for type III Wald chi-square test for diversity measures with savanna (broadleaf savanna and fine-leaf savanna) and invasion gradient (remnant and uninvaded) as fixed effects and site as a random effect

Response	**Effects**	χ^2	***df***	***p* value**
a) Richness	Intercept	87.445	1	<2e-16
	Savanna	0.959	1	0.327
	Invasion gradient	0.128	1	0.72
	Savanna × Invasion gradient	0.195	1	0.659
b) Evenness	Intercept	120.995	1	<2e-16
	Savanna	1.096	1	0.295
	Invasion gradient	0.622	1	0.43
	Savanna × Invasion gradient	0.320	1	0.571
c) Shannon diversity	Intercept	101.975	1	<2e-16
	Savanna	0.238	1	0.625
	Invasion gradient	0.608	1	0.435
	Savanna × Invasion gradient	0.478	1	0.489

Table S4: Difference between entire community and native community for: a) richness; b) evenness; and, c) Shannon diversity. The results presented are *p*-values from type III Wald chi-square test for diversity measures with savanna and invasion gradient as fixed effects and site as a random effect

Response	**Effect**	**All species (*p* value)**	**Native species (*p* value)**
a) Richness	Savanna	0.041	0.081
	Invasion gradient	< 2.2e-16	< 2.2e-16
	Savanna × Invasion gradient	0.003	0.010
b) Evenness	Savanna	0.429	0.057
	Invasion gradient	0.002	0.106
	Savanna × Invasion gradient	0.114	0.891
c) Shannon Diversity	Savanna	0.146	0.008
	Invasion gradient	0.097	0.048
	Savanna × Invasion gradient	0.981	0.287

Table S5: Model selection parameter (AIC scores) used to choose between linear and polynomial fits. Linear and second degree polynomial fits for different metrics of alpha diversity were tested across a continuous gradient of invasion. The diversity metrics examined were: a) richness; b) evenness; and, c) Shannon diversity

Response	**Savanna type**	**AIC Score** (Linear model)	**AIC Score** (Polynomial model)
a) Richness	BLS	354.638	361.002
	FLS	239.782	259.143
b) Evenness	BLS	-25.432	-6.682
	FLS	-23.574	-1.697
c) Shannon diversity	BLS	87.646	106.393
	FLS	67.016	86.815

Table S6: Abundance based composition (bray dissimilarity) across invasion gradient in two savannas. The results presented are of PERMANOVA model for abundance based composition with savanna type and invasion gradient as fixed effects

Effects	***df***	**SS**	**r^2**	***F***	***p* value**
Savanna	1	3.872	0.071	13.656	0.001
Invasion gradient	4	6.54	0.012	5.766	0.001
Savanna × Invasion gradient	4	2.677	0.049	2.36	0.001
Residual	146	41.394	0.759		
Total	155	54.483	1		

Table S7: Direction and strength of change in abundance of species across invasion gradient in BLS. The list includes **s**pecies with significant contribution ($p<0.05$) to the observed abundance based (bray dissimilarity) compositional change. Species marked with * represents the Indicator species of old growth savannas

Species	**Life form**	**Nativity**	**NMDS1**	**NMDS2**	**r^2**
*Hetreropogon contortus**	Grass	Native	-0.932	-0.362	0.289
Rostellularia procumbens	Forb	Native	-0.135	0.991	0.272
*Chrysopogon fulvus**	Grass	Native	-0.485	0.874	0.248
*Apluda mutica**	Grass	Native	0.827	0.562	0.243
*Sehima nervosa**	Grass	Native	-0.117	0.993	0.237
Spermacoce pusilla	Forb	Native	-0.990	0.144	0.214
*Lavandula bipinnata**	Forb	Native	0.068	0.998	0.213
*Cyanotis fasciculata**	Forb	Native	-0.263	0.965	0.190
Urena lobata	Forb	Native	-0.043	-0.999	0.175
Dicanthium pursutum	Grass	Native	-0.565	-0.825	0.174
Curculigo orchioides	Forb	Native	0.864	0.504	0.164
*Melanocenchris jacquemontii**	Grass	Native	-0.734	0.679	0.164
Indigofera linifolia	Forb	Native	-0.959	-0.284	0.156
Polygala arvensis	Forb	Native	-0.982	-0.191	0.151
Tephrosia pumila	Subshrub	Native	-0.218	-0.976	0.147
Vigna trilobata	Forb	Native	-0.623	0.782	0.146
Crotalaria hebecarpa	Forb	Native	-0.593	-0.805	0.140
Zornia gibbosa	Forb	Native	-0.763	0.646	0.136
Sporobolus indicus	Grass	Native	-0.965	-0.263	0.134
Parasopubia delphiniifolia	Forb	Native	-0.725	0.689	0.129
Vigna sublobata	Forb	Native	-0.148	-0.989	0.129
Alternanthera sessilis	Forb	Invasive	0.347	-0.938	0.123
Alysicarpus vaginalis	Forb	Native	-0.374	-0.928	0.122
*Tripogon bromoides**	Grass	Native	-0.894	0.447	0.118
Bidens pilosa	Forb	Invasive	0.954	0.301	0.118
Emilia sonchifolia	Forb	Invasive	0.566	0.824	0.112
Aristida redacta	Grass	Native	-0.998	0.055	0.110
Phyllanthus amarus	Forb	Native	-0.307	-0.952	0.108
Alysicarpus tetragonolobus	Forb	Native	-0.941	-0.338	0.107
Polygala erioptera	Forb	Native	-0.785	0.619	0.106
Sida acuta	Forb	Native	0.216	-0.976	0.106
Abutilon indicum	Forb	Native	0.220	-0.976	0.104
Lophopogon tridentatus	Grass	Native	-0.960	0.280	0.100

Table S7 continued

Species	Life form	Nativity	NMDS1	NMDS2	r^2
Aristida stocksii	Grass	Native	-0.633	0.774	0.099
Indigofera astragalina	Forb	Native	0.127	-0.992	0.098
Chromolaena odorata	Subshrub	Invasive	0.172	-0.985	0.096
Andropogon pumilus	Grass	Native	-0.918	0.397	0.096
Dactyloptenium aegypticum	Grass	Native	-0.291	-0.957	0.093
striga lutea	Forb	Native	-0.150	0.989	0.093
Oplismenus burmanni	Grass	Native	0.830	0.558	0.092
Panicum trypheron	Grass	Native	-0.269	0.963	0.089
Urochloa ramosa	Grass	Native	-0.178	-0.984	0.088
Cynarospermum asperrimum	Forb	Native	0.721	0.693	0.086
Digitaria abludens	Grass	Native	-0.279	-0.960	0.086
Pulicaria wightiana	Forb	Native	-0.790	0.614	0.086
Senna uniflora	Forb	Invasive	0.101	-0.995	0.080
Digitaria stricta	Grass	Native	-0.868	0.497	0.079
Striga densiflora	Forb	Native	-0.966	0.260	0.079
Biophytum sensitivum	Forb	Native	-0.386	-0.923	0.078

Table S8: Direction and strength of change in abundance of species across invasion gradient in FLS. The list includes species with significant contribution ($p<0.05$) to the observed abundance based (bray dissimilarity) compositional change. Species marked with * represents the Indicator species of old growth savannas

Species	Life form	Nativity	NMDS1	NMDS2	r^2
Parthenium hysterophorus	Forb	Invasive	-0.996	0.086	0.408
Senna uniflora	Forb	Invasive	0.549	0.836	0.389
*Apluda mutica**	Grass	Native	0.602	0.798	0.328
Urochloa ramosa	Grass	Native	-0.999	0.043	0.326
Triumfetta rhomboidea	Forb	Invasive	0.528	0.849	0.288
*Hetreropogon contortus**	Grass	Native	0.962	-0.273	0.239
Themeda quadrivalvis	Grass	Native	0.434	0.901	0.227
Alternanthera sessilis	Forb	Invasive	-0.958	0.285	0.198
Chamaecrista mimosoides	Forb	Native	0.690	0.724	0.195
*Chrysopogon fulvus**	Grass	Native	0.131	-0.991	0.192
*Cyanotis fasciculata**	Forb	Native	0.362	-0.932	0.187
Euphorbia heterophylla	Forb	Invasive	0.365	0.931	0.179
Aristida stocksii	Grass	Native	0.119	-0.993	0.169
Dactyloptenium aegypticum	Grass	Native	-0.980	-0.201	0.159
*Melanocenchris jacquemontii**	Grass	Native	0.368	-0.930	0.157
Striga densiflora	Forb	Native	0.078	-0.997	0.154
Pulicaria wightiana	Forb	Native	0.747	0.664	0.146
Tetrapogon tenellus	Grass	Native	-0.960	0.281	0.142
Vigna trilobata	Forb	Native	0.115	-0.993	0.137
Polygala arvensis	Forb	Native	-0.452	-0.892	0.131
Striga asiatica	Forb	Native	0.990	0.141	0.131
Bidens pilosa	Forb	Invasive	-0.643	0.766	0.128
Echinochloa colona	Grass	Native	-0.951	0.309	0.119
Dicanthium foveolatum	Grass	Native	-0.998	0.065	0.116
Rostellularia procumbens	Forb	Native	-0.943	-0.332	0.105
aerva lanata	Forb	Native	-0.533	0.846	0.103
Synedrella nodiflora	Forb	Invasive	0.333	0.943	0.102
Evolvulus alsinoides	Forb	Native	-0.386	-0.922	0.102
Setaria pumila	Grass	Native	-0.936	0.353	0.101
Lepidagathis cristata	Forb	Native	0.066	-0.998	0.100
Gomphrena	Forb	Native	0.300	0.954	0.098
Unknown 1	Forb	Native	0.307	0.952	0.094
Unknown 2	Forb	Native	0.307	0.952	0.094
Acalypha indica	Forb	Native	-0.924	0.383	0.085

Table S8 continued

Species	Life form	Nativity	NMDS1	NMDS2	r^2
Tribulus terrestris	Forb	Native	-0.998	0.059	0.085
*Leucas aspera**	Forb	Native	-0.998	-0.059	0.083
Cyperus rotundus	Sedge	Native	-0.874	0.485	0.081
Crotalaria hebecarpa	Forb	Native	0.078	-0.997	0.081
Achyranthes aspera	Forb	Native	-0.640	0.768	0.080
Zornia gibbosa	Forb	Native	0.908	-0.418	0.080
Lagascea mollis	Forb	Invasive	-0.730	0.684	0.078
Cyperus pumilus	Sedge	Native	-0.803	-0.596	0.078
Ipomoea eriocarpa	Forb	Native	0.911	0.412	0.077
Xanthium strumarium	Forb	Invasive	-0.962	0.273	0.074
Dicanthium pursutum	Grass	Native	-0.993	-0.117	0.070

Table S9: Incidence based compositional differences (Sorenson dissimilarity) between uninvaded and invaded plots in the two savannas. The results presented are for type III Wald chi-square test for dissimilarity with savanna type and invasion gradient as fixed effects and site as a random effect

Response	**Effects**	χ^2	***df***	***p* value**
Dissimilarity	Intercept	96.742	1	2.20E-16
	Savanna	0.027	1	0.869
	Invasion gradient	70.618	2	4.63E-16
	Savanna × Invasion gradient	1.538	2	0.464

Table S10: Incidence based composition (Sorenson dissimilarity) across invasion gradient in two savannas. The results presented are of PERMANOVA model for incidence based composition with savanna type and invasion gradient as fixed effects

Effects	***df***	**SS**	**r^2**	***F***	***p* value**
Savanna	1	4.497	0.107	21.788	0.001
Invasion gradient	4	5.695	0.136	6.898	0.001
Savanna × Invasion gradient	4	1.534	0.036	1.858	0.001
Residual	146	30.133	0.719		
Total	155	41.859	1		

Table S11: Difference between remnant and uninvaded plots in incidence based compositional dissimilarity in two savannas. Welsh two sample t test on the difference of: a) incidence based dissimilarity (Sorenson dissimilarity); b) turnover; and, c) nestedness in broadleaf savanna and fine-leaf savanna

Variable	***t* value**	***df***	***p* value**
a) Dissimilarity	1.235	22.785	0.229
b) Turnover	0.012	23.746	0.989
c) Nestedness	1.704	21.54	0.102

Table S12: Difference between remnant and uninvaded plots in abundance based compositional dissimilarity in two savannas. Welsh two sample t test on the difference of: a) abundance based dissimilarity (bray dissimilarity); b) turnover; and, c) nestedness in broadleaf savanna and fine-leaf savanna

Response	***t* value**	***df***	***p* value**
a) Dissimilarity	1.115	28.966	0.273
b) Turnover	1.112	28.879	0.275
c) Nestedness	-0.422	22.015	0.676

Table S13: Differences between entire community and native community for: a) abundance based dissimilarity (bray dissimilarity); b) turnover; and, c) nestedness. The results presented are *p* values from type III Wald chi-square test for dissimilarity with savanna type and invasion gradient as fixed effects and site as a random effect

Response	Fixed effects	All species (*p* value)	Native species (*p* value)
a) Dissimilarity	Savanna	< 4.92e-04	1.08E-04
	Invasion gradient	2.28E-14	1.35E-13
	Savanna × Invasion gradient	0.015	0.014
b) Turnover	Savanna	0.001	1.67E-04
	Invasion gradient	0.005	0.014
	Savanna × Invasion gradient	0.663	0.295
c) Nestedness	Savanna	0.212	0.099
	Invasion gradient	0.003	0.002
	Savanna × Invasion gradient	0.199	0.692

Table S14: Incidence based beta diversity across invasion gradient in the two savannas. The results presented are for type III Wald chi-square test for beta diversity with savanna type and invasion gradient as fixed effects and site as a random effect

Response	**Effects**	χ^2	***df***	***p* value**
Beta diversity	Intercept	272.433	1	2.20E-16
	Savanna	0.001	1	0.974
	Invasion gradient	17.517	3	0.001
	Savanna × Invasion gradient	4.245	3	0.236

Table S15: Difference between remnant and uninvaded plots for: a) incidence based beta diversity; and its components b) turnover; and, c) nestedness. The results presented are for type III Wald chi-square test for beta diversity and its components with savanna type and invasion gradient as fixed effects and site as a random effect

Response	**Effects**	χ^2	***df***	***p* value**
a) Beta diversity	Intercept	218.447	1	<2e-16
	Savanna	0.382	1	0.537
	Invasion gradient	0.124	1	0.724
	Savanna × Invasion gradient	0.119	1	0.730
b) Turnover	Intercept	164.558	1	<2e-16
	Savanna	0.169	1	0.681
	Invasion gradient	0.093	1	0.761
	Savanna × Invasion gradient	0.019	1	0.890
c) Nestedness	Intercept	11.825	1	5.84E-04
	Savanna	0.090	1	0.7644
	Invasion gradient	2.150	1	0.1425
	Savanna × Invasion gradient	0.114	1	0.7359

Table S16: Difference between remnant and uninvaded plots for: a) abundance based beta diversity; and its components b) turnover; and, c) nestedness. The results presented are type III Wald chi-square test for abundance based beta diversity and its components with savanna type and invasion gradient as fixed effects and site as a random effect

Response	**Effects**	χ^2	***df***	***p* value**
a) Beta diversity	Intercept	147.473	1	<2e-16
	Savanna	0.181	1	0.670
	Invasion gradient	1.447	1	0.229
	Savanna × Invasion gradient	0.007	1	0.934
b) Turnover	Intercept	89.314	1	<2e-16
	Savanna	0.005	1	0.946
	Invasion gradient	1.033	1	0.310
	Savanna × Invasion gradient	0.288	1	0.592
c) Nestedness	Intercept	9.677	1	1.87E-03
	Savanna	0.304	1	0.581
	Invasion gradient	0.003	1	0.958
	Savanna × Invasion gradient	1.495	1	0.221

Table S17: Difference between entire community and native community in abundance based beta diversity and its components across invasion gradient in the two savannas. The results presented are *p*-values from a type III Wald chi-square test for: a) abundance based beta diversity; b) turnover; and, c) nestedness with savanna type and invasion gradient as fixed effects and site as a random effect

Response	Effects	All species (*p* value)	Native species (*p* value)
a) Beta diversity	Savanna	0.259	0.323
	Invasion gradient	0.000	0.008
	Savanna × Invasion gradient	0.001	0.172
b) Turnover	Savanna	0.705	0.734
	Invasion gradient	0.666	0.667
	Savanna × Invasion gradient	0.005	0.435
c) Nestedness	Savanna	0.486	0.510
	Invasion gradient	0.030	0.018
	Savanna × Invasion gradient	0.815	0.631

Table S18: Change in diversity across invasion gradient in fine-leaf savanna with invaders of different lifeforms. The results presented are for type III Wald chi-square test for: a) richness; b) evenness; and, c) Shannon diversity with invader lifeform and invasion gradient as fixed effects and site as a random effect

Response	**Effects**	χ^2	***df***	***p* value**
a) Richness	Invader life form	1.107	1	0.29
	Invasion gradient	34.151	3	8.41 E-07
	Invader life form × Invasion gradient	3.072	3	0.38
b) Evenness	Invader life form	1.554	1	0.213
	Invasion gradient	2.262	3	0.519
	Invader life form × Invasion gradient	4.968	3	0.174
c) Shannon diversity	Invader life form	1.497	1	0.221
	Invasion gradient	7.123	3	0.068
	Invader life form × Invasion gradient	4.026	3	0.258

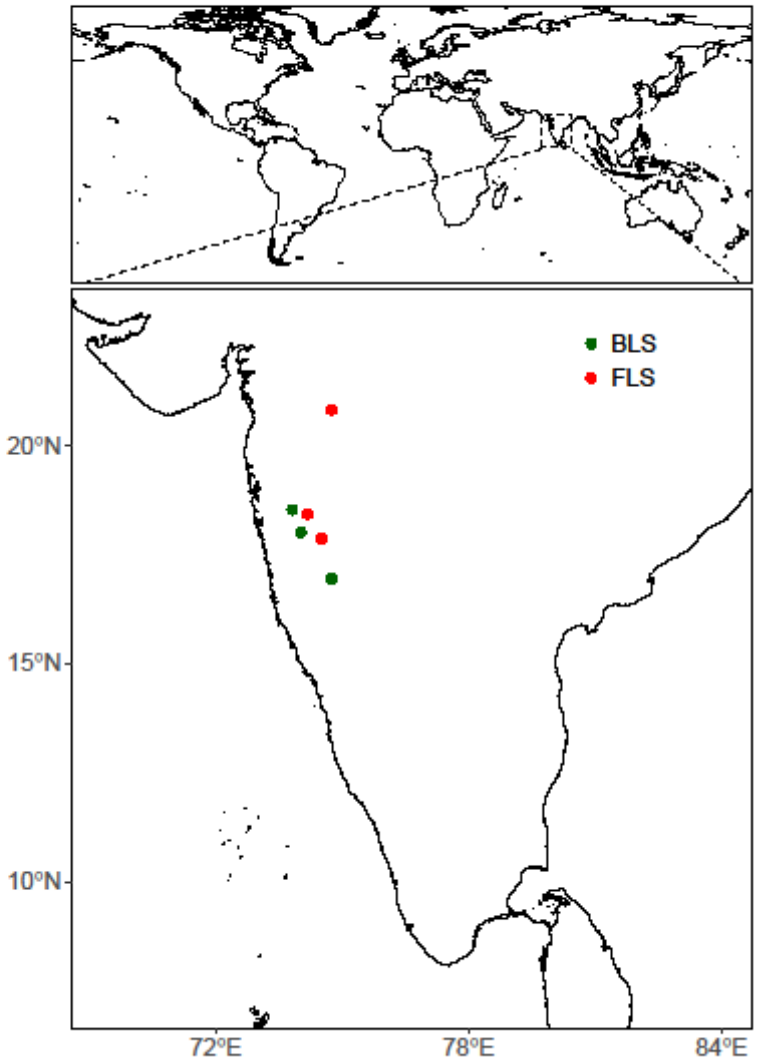

Figure S1: Location of study site in the Indian subcontinent (broadleaf savanna – green, fine-leaf savanna – red).

Broadleaf savanna

Fine-leaf savanna

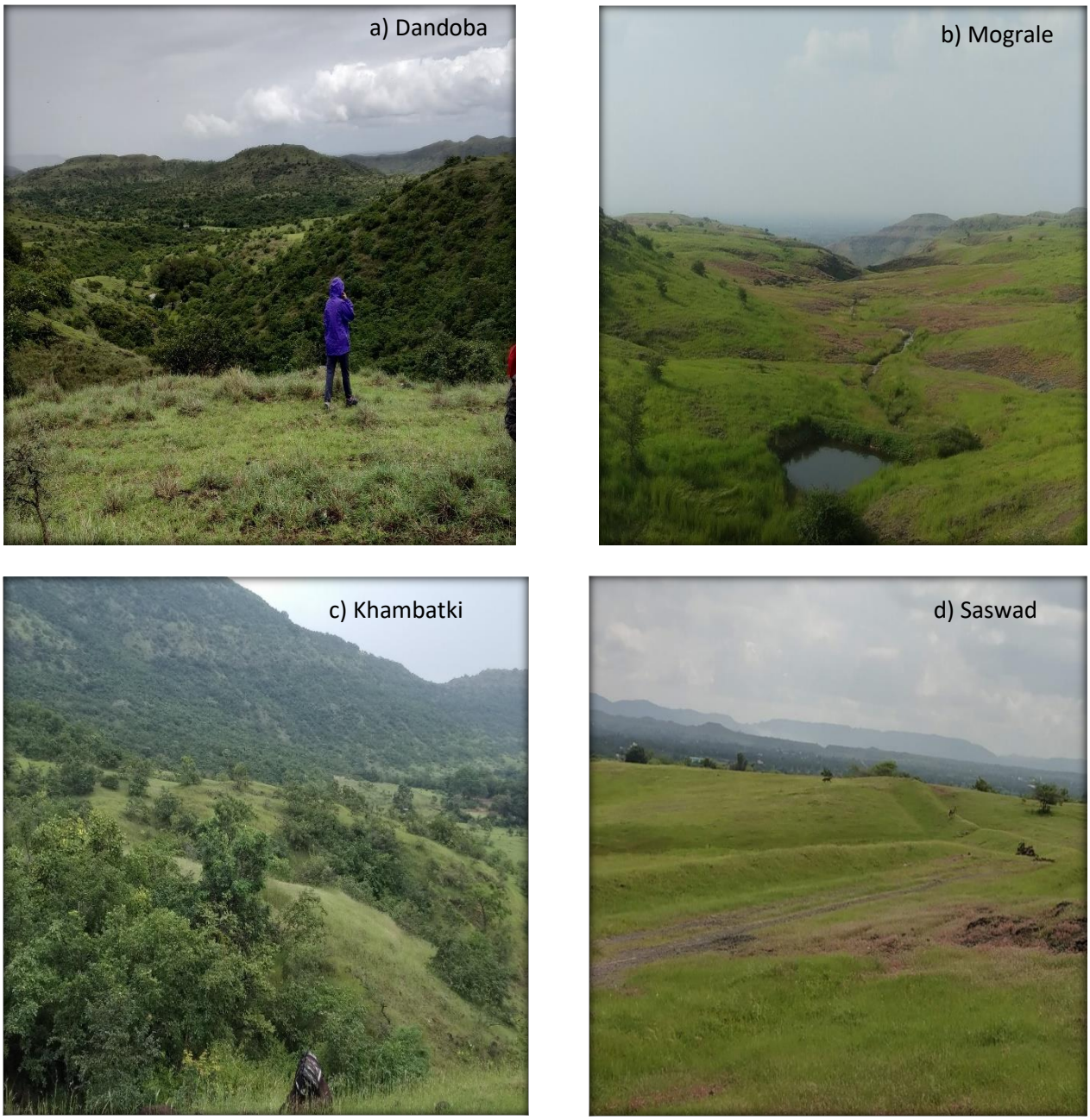

Figure S2: Representative images of broadleaf savanna sites: a) Dandoba; and, c) Khambatki and fine-leaf savanna sites: b) Mograle; and, d) Saswad in savannas of western Maharashtra in India.

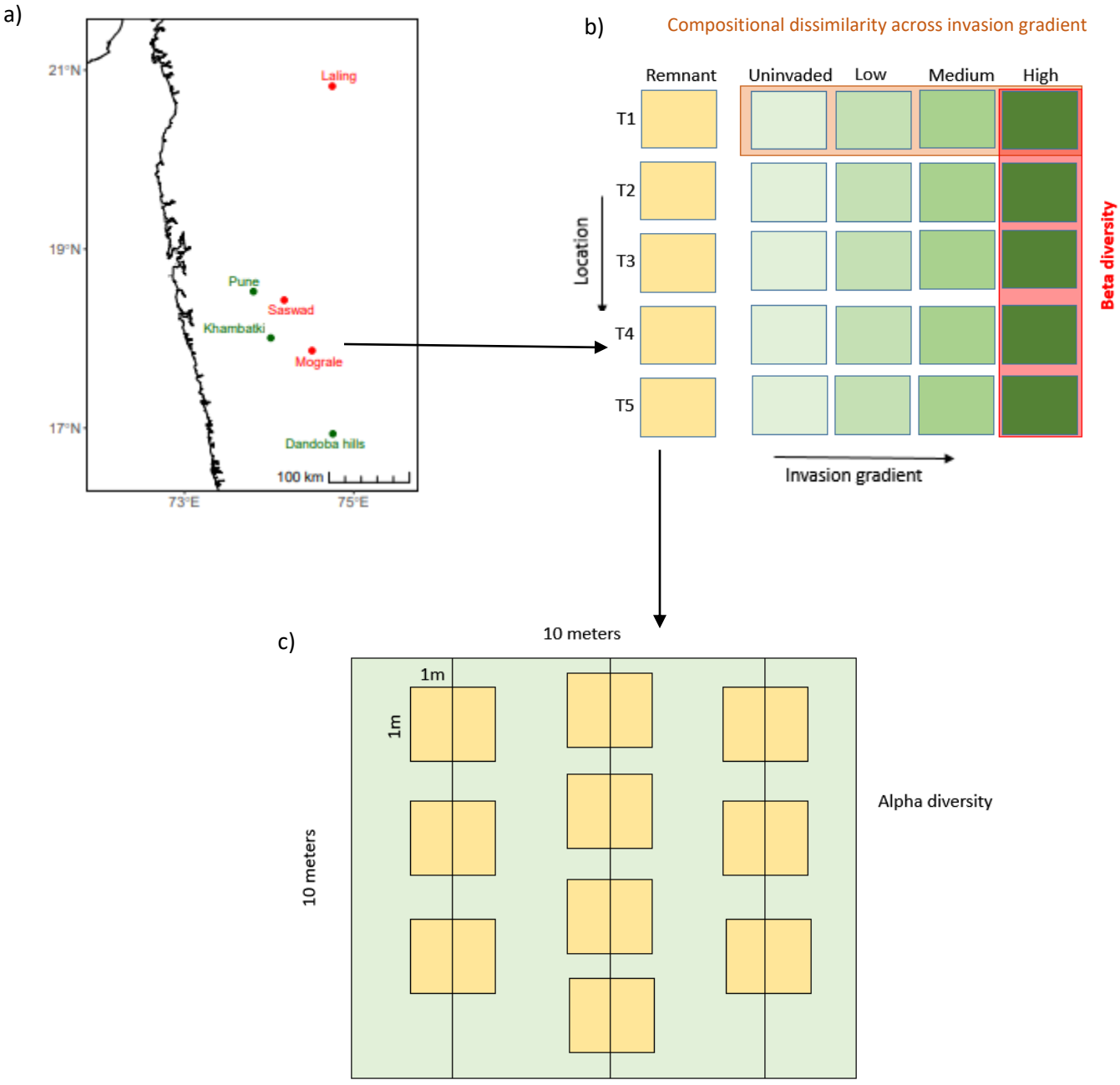

Figure S3: Study design showing: a) three broadleaf savanna sites (Green) and three fine-leaf savanna sites (Red) on a scaled map; b) five locations along an invasion gradient in each site. Locations were not always located in a linear fashion as shown in the representative image and minimum distance between two locations was 300 meters. c) Smaller 1m x1m quadrats within each 10x10m plot to estimate alpha diversity.

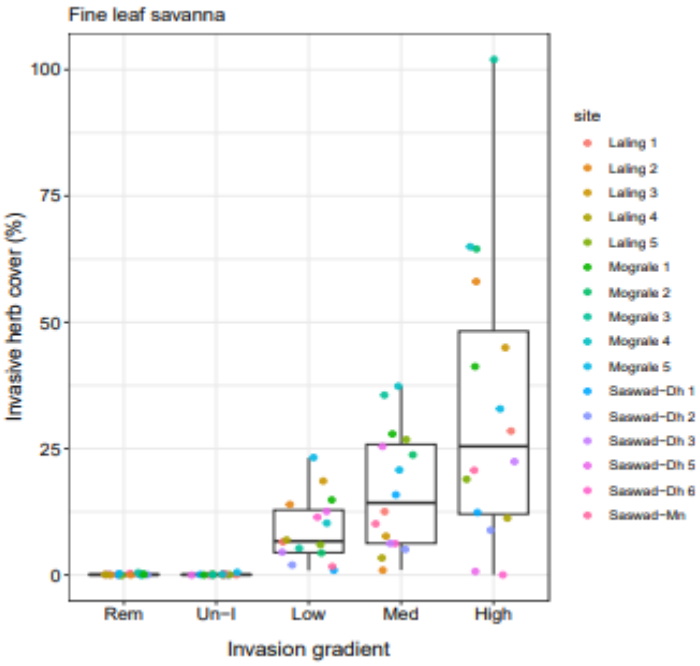

Figure S4: Cover of all herbaceous invasive species in fine-leaf savanna measured as percent cover/m^2. Each point represents one 10 ×10 m^2 plot.

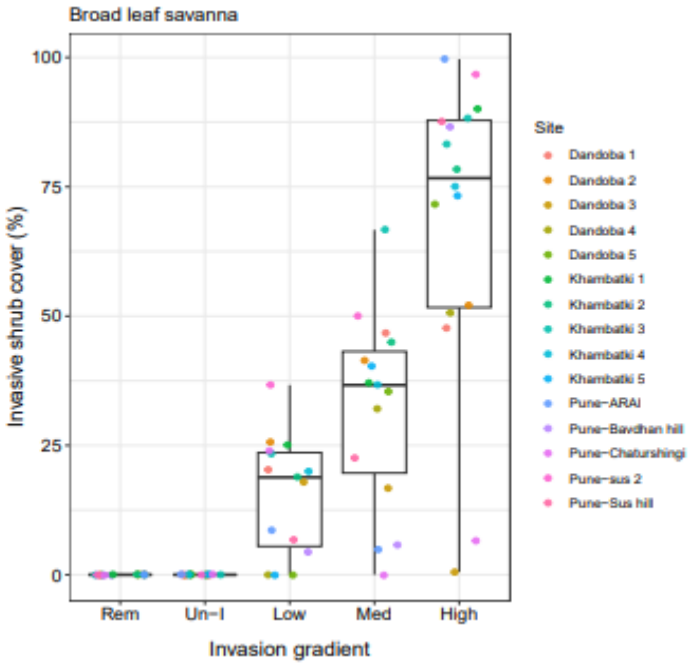

Figure S5: Cover of all invasive shrubs in broadleaf savanna measured as percent cover/m. Each point represents one 10 × 10 m^2 plot.

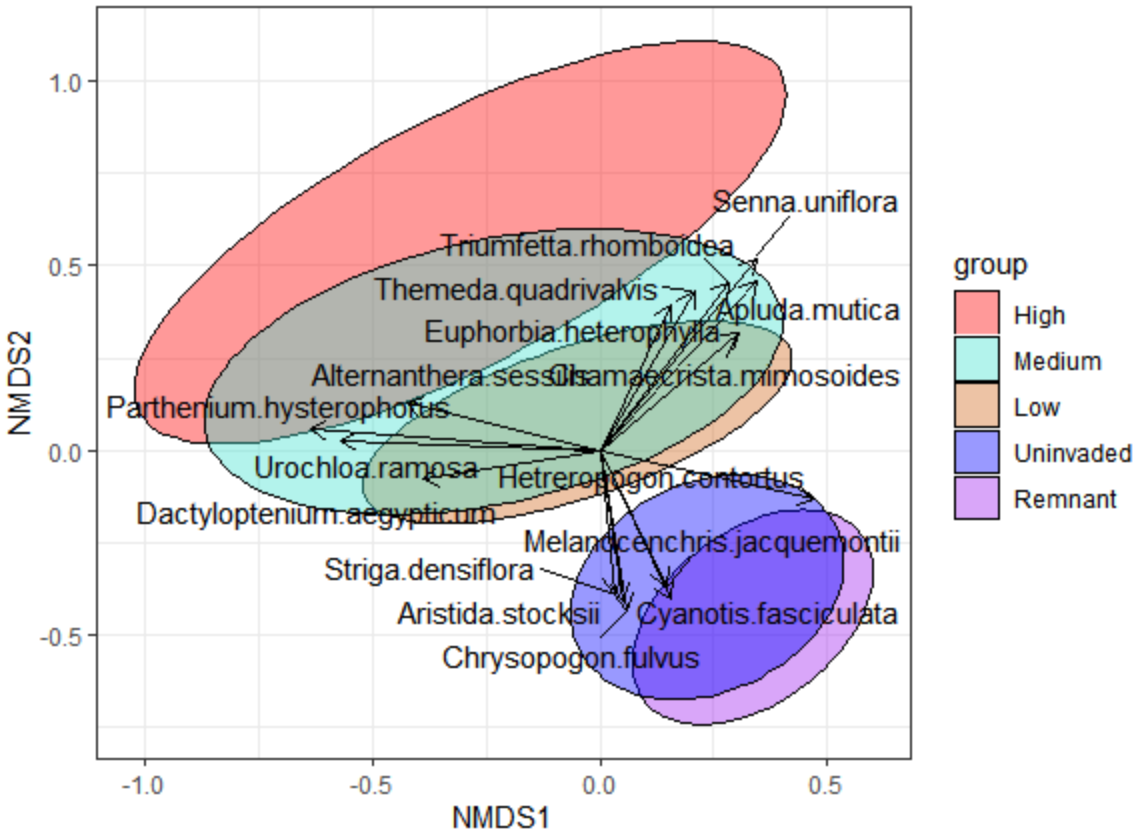

Figure S6: Direction of change in abundance of species of fine-leaf savanna in the NMDS ordination space. The length of the vector indicate the strength of the change in a particular direction. Only the species with $r^2>0.15$ and $p < 0.05$ are shown here. Ellipses represent 95% SE for each invasion level.

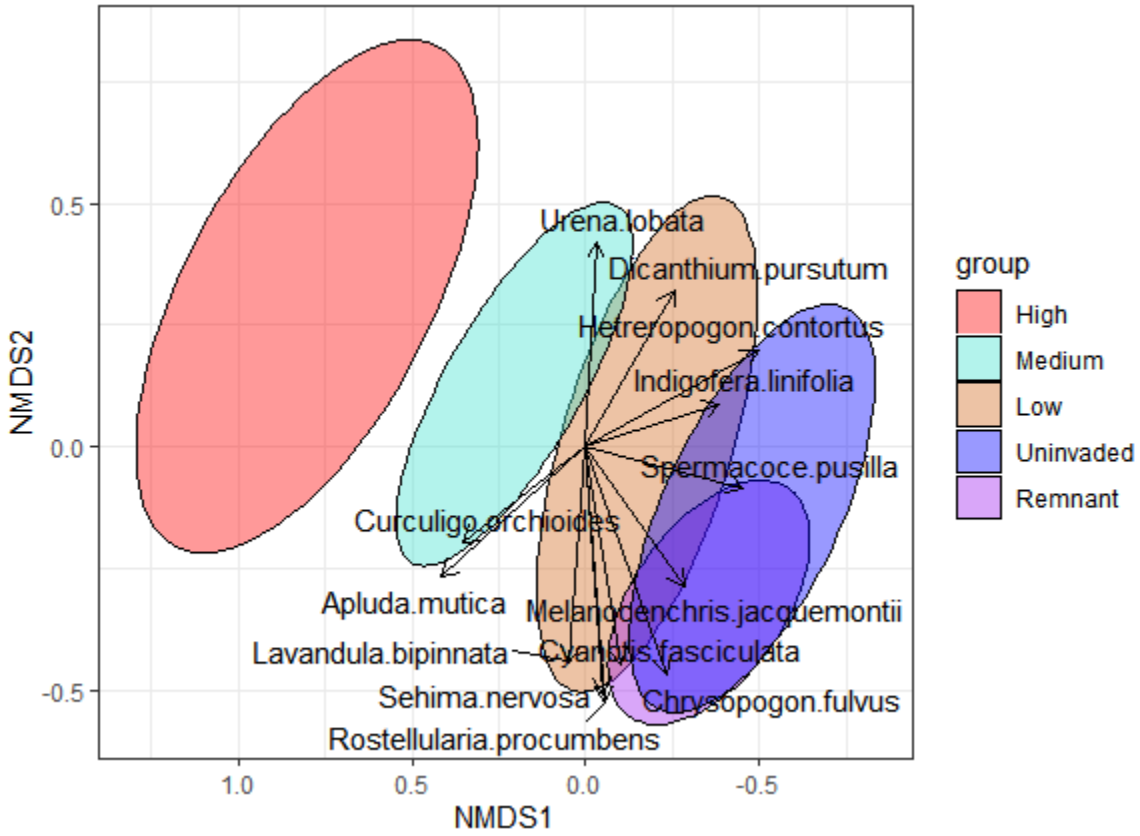

Figure S7: Direction of change in abundance of species of broadleaf savanna in the NMDS ordination space. The length of the vector indicate the strength of the change in a particular direction. Only the species with $r^2 > 0.15$ and $p < 0.05$ are shown here. Ellipses represent 95% SE for each invasion level.

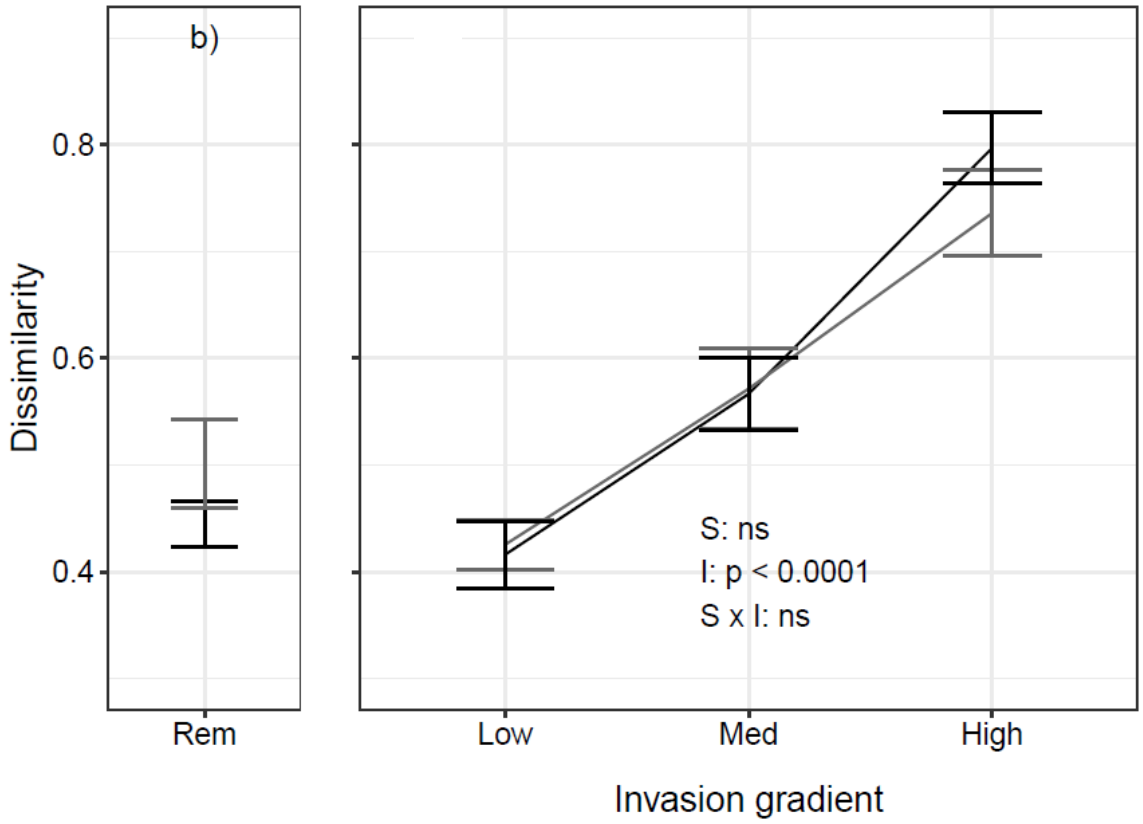

Figure S8: Incidence based compositional dissimilarity (Sorenson) between uninvaded and invaded plots**.** Gray lines represent FLS and black lines represent BLS. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S x I - Savanna type and Invasion gradient interaction.

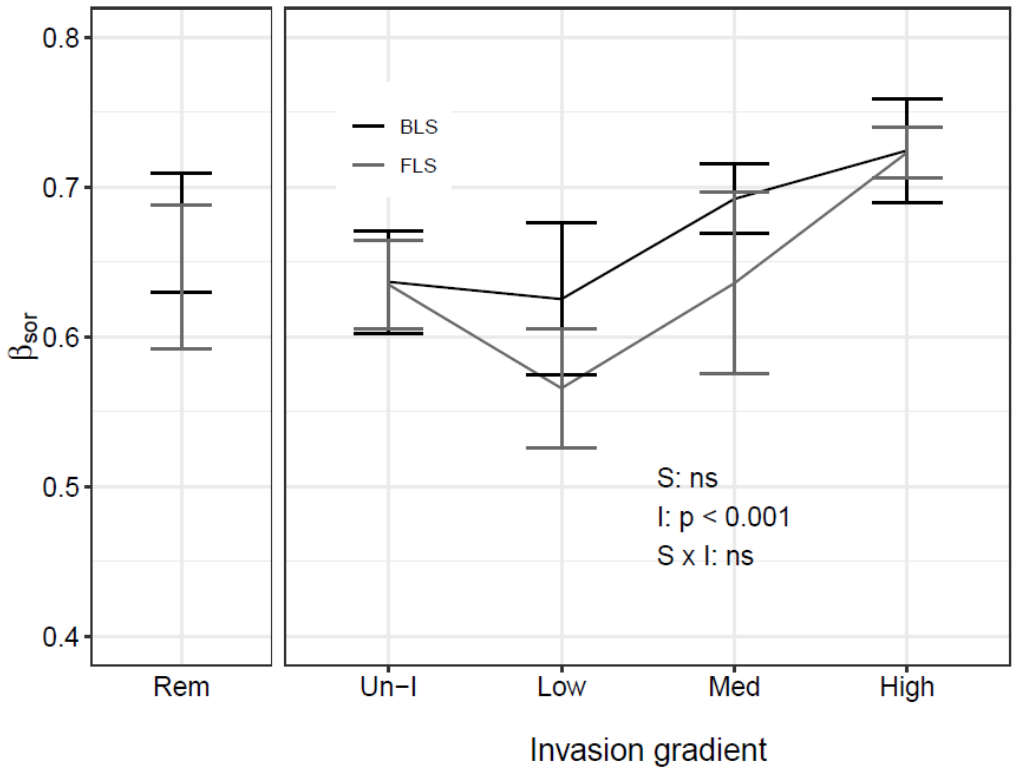

Figure S9: Incidence based beta diversity for each site across invasion gradien**t.** Gray lines represent FLS and black lines represent BLS. Rem - Remnant plots which represents old growth savannas; Un-I - uninvaded plots with had minimal invasion; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

Chapter 5: Shift in functional and phylogenetic composition of plant communities across invasion gradient in savannas

Introduction

Invasion by non-native species can change functional composition of communities which can further lead to changes in ecosystem functions and services (Lobo et al. 2023; Abreu and Durigan 2011; Sodhi et al. 2019). Therefore, it is important to understand these changes in functional composition to accurately predict the impacts of invaders on higher level biodiversity processes. Community weighted trait means and functional diversity metrics are frequently used to quantify the changes in functional composition of communities caused by invasion (Sodhi et al. 2019; Gallien and Carboni 2017). These changes can also provide mechanistic understanding of establishment and impact of invasive species in an area (Loiola et al. 2018). Research from temperate grasslands have shown varying effects of invasion on both functional and phylogenetic diversity. But the understanding of the invaders impact on functional diversity from tropics is sparse. In third chapter of this thesis, I showed that, invasive species have traits associated with faster resource acquisition and greater competitive abilities than the native community. Moreover, findings from Chapter 4 indicate that invaded communities in savannas e^{x}hibit distinct species compositions compared to uninvaded communities. Given these results, I expect that invasion will cause changes in functional composition of savanna communities. I expect the invaded systems to have faster resource use and competitive ability which would consequently lead to increased rates of nutrient cycling in these savannas (Rothstein et al. 2004).

Functional traits are defined as quantifiable feature of plants that directly related to their growth survival and reproduction (Violle et al. 2007). These traits provide mechanistic links to vital

ecosystem functions and services. Furthermore, these traits influence the establishment of a species in a community, by mediating its interaction with environmental and biotic filters (Laughlin et al. 2020). Functional traits measured at individual level, can be scaled up to community level by quantifying community weighted trait means. These identify dominant trait values in a community which can provide insights into community level properties such as ecosystem functions (Jing et al. 2019). Invasive species are known to be more competitive and acquisitive in resource use and therefore are taller, have higher stem width, high leaf nitrogen, lower LMA (Kleunen et al. 2010). Determining how invasion leads to change in functional traits of community is critical in understanding their potential impact on ecosystem functioning. For instance, lower LMA and higher nitrogen content can lead to faster nutrient cycling and rapid resource turnovers in an ecosystem (Ehrenfeld 2003). Such alterations can further lead to increase in productivity and replacement of species which thrives in nutrient poor environments (Carboni et al. 2021). However, quantifying shifts in single traits to infer community level processes can be limited due to trait correlations. Such correlations can come about if these traits are mechanistically linked (biophysical constraint) or due to correlated selection of these traits (Díaz et al. 2016). Most of the variation amongst extant vascular plants are along the two major trait axis which are related to distinct ecological strategies. First axis is associated with traits corresponding to resource use strategies such as leaf mass per unit area (LMA) and leaf nitrogen content (LNC) and the second axis is associated with traits related to competitive ability such as height (H_{max}) and reproductive output such as Seed mass (Westoby et al. 2002; Díaz et al. 2016). It is therefore important to study traits in a multidimensional space, as that captures trait tradeoffs and provides a better representation community level impact (Kraft et al. 2015).

Along with impact on ecosystem level functions, studying the trait compositions of communities can also provide insights into mechanism of community assembly (Chesson 2000). Niche theory assumes that different ecological filters will leave a detectable signal on the functional traits of the species (Webb et al. 2002). This would mean that species with similar traits will have overlapping niche, whereas those with differences in traits will occupy different niche. However, in environments where communities are limited by single resource, trait dissimilarities reflect differences in competitive ability and not niche differences (Funk and Wolf 2016). Species can invade a regions by either occupying pre-existing niche or by niche expansion (Loiola et al. 2018; Hejda and Bello 2013). These two different mechanisms can be detected by quantifying the shifts in the community weighted trait means (Sodhi et al. 2019).

Using a trait based approach also allows us to quantify metrics of diversity at the community level. Several functional diversity metrics have been developed to get a more complete understanding of functional structure of a community. There are three major components of functional diversity: richness, evenness, and divergence (Gallien and Carboni 2017). Functional richness measures the multidimensional trait volume occupied by a community. Functional evenness quantifies the distribution of abundance within the community trait space. Functional divergence measures if the distribution of species and their abundances are towards the intermediate or extreme trait values (Villéger et al. 2008).

A comprehensive understanding of diversity of a community encompasses studying variations in organisms at different levels including genetic variability. Phylogenetic diversity provides information on genetic variability within a community (Tucker and Cadotte 2013). Additionally,

Collection of trait data to estimate functional diversity is often laborious and limited and therefore, phylogenetic diversity are often also used as a proxy for trait/ niche space occupied by the species (Jin and Qian 2022; Gallien and Carboni 2017). Similar to functional diversity, phylogenetic diversity is measured by quantifying the mean phylogenetic distance between all the species of community (MPD) (Webb et al. 2002). Furthermore, mean pairwise distance can be used to derive net relatedness index (NRI) which is frequently used to compare phylogenetic diversity between communities. Positive NRI values indicate phylogenetic clustering, higher the value more clustered the communities are than expected by chance (Webb et al. 2002). Using phylogenetic diversity as a proxy for functional diversity is based on an underlying assumption that phylogenetically close species share similar traits than phylogenetically distant species. However, using such strong assumption may have certain shortcomings (Gallien and Carboni 2017). It is therefore important to first establish a relationship between functional and phylogenetic diversity whenever possible by quantifying functional mean pairwise distances (fMPD) and Phylogenetic Mean pairwise distance (PdMPD) (Cadotte et al. 2019).

The results from the previous chapter show that the impact of invasion on taxonomic diversity and composition differs in the two savannas. Since the lifeform and therefore the trait syndrome of major invaders differs across the two savannas, I hypothesize differential impact of invasion on functional and phylogenetic diversity in these savannas. Trait shifts caused by invasion can not only have consequences on ecosystem level functions but can also provide insights into the mechanism of invasion. To test this, in this chapter I quantified the impact of invasion on: a) community weighted trait means; b) functional diversity; and, c) phylogenetic diversity of herbaceous communities across an invasion gradient in two types of savannas. Furthermore,

functional and phylogenetic diversity of dominant species were compared to test if phylogenetic diversity can be used as a proxy for functional diversity in these systems. Finally, I measured the phylogenetic and functional beta diversity, to understand if the impact of invasion on PD and FD at higher spatial scales, are similar to changes in taxonomic diversity as measured in the previous chapter.

Methods

Collection of species

For each 155, 10m x10m plot studied across the invasion gradient in both savannas, the relative percent cover of all herbaceous species was quantified. Five to ten individuals, for each species which constituted 90% of total vegetation cover in each plot were collected. On average species representing 90% vegetative cover of the 10m x 10m plot were collected. In total 39 herbaceous species from broad leaf savanna and 49 species from fine leaf savanna were collected for trait quantification.

Trait collection and quantification

Thirteen traits associated with plant's growth, survival and reproduction in savannas were identified. Six continuous whole plant and leaf traits from a minimum of five individuals for each species were quantified. This consisted of four leaf level traits: leaf area (LA), leaf dry matter content (LDMC), leaf mass per unit area (LMA) and percent lead nitrogen content (% N) and two whole plant level trait height and stem diameter. Additionally field observations, global trait database (TRY), Floras and other published papers were referred to get information of the remaining seven qualitative traits. These traits were, type of belowground bud bank (Pausas et al.

2018), Photosynthetic pathways (C3 vs C4), Seed volume, lifespan(annual, annual to perennial, perennial), nitrogen fixer, lifeform (herb vs shrub vs tree), architecture (erect vs prostrate). To estimate the leaf traits, fresh weight, dry weight and leaf area for five leaves of each individual were measured. First, the fresh weight of species was quantified followed by oven drying them at 80 degrees for 3 days, after which dry leaf samples were weighed. LDMC was then quantified by dividing the fresh weight with the dry weight of the leaf. Leaf area was measured and estimated by using image j software. Dry weight divided by the total area measured was used to estimate the LMA. Stem diameter was measured at one-third distance from the bottom using the digital screw gauge (Harguindeguy et al. 2013). Finally, I used oven dried finely ground leaf samples to estimate the total nitrogen content for three individuals of each species using FLASHSMART CNHS/O analyzer.

Community weighted trait- univariate and multivariate

To understand the shift in trait combination of community across invasion gradient, changes in community weighted traits with invasion in two savannas were studied. Since, traits can often be correlated or shift in one trait can override other traits, it is crucial to estimate these changes in multidimensional trait space. Community weighted traits associated with competition (height and leaf area), resource acquisition (LDMC, LMA), reproductive ability (Seed volume) and stem diameter were quantified for each 10m x 10m plot. This was done by multiplying the mean trait value of the species with its relative abundance in the community. This exercise was done both for the entire herbaceous community and only for the native herbaceous community. A set of mixed effect models were performed using various community weighted traits as response variable, savanna type and invasion gradient as fixed effect and each site as a random effect. An

additional glmm was performed to test if remnant communities differ from uninvaded communities. Finally, to quantify differences in multidimensional space, I used community weighted mean for six traits for all the 155 plots and performed Principal component analysis (PCA) by using factoextra package (Kassambara and Mundt 2020). To test statistical differences in multidimensional trait composition along invasion gradient in the two savannas I performed PERMANOVA analysis using adonis2 function in vegan package in R.

Functional diversity

Functional diversity metrics : functional richness, functional evenness and functional divergence for each community were quantified using FD package (Laliberté et al. 2023). Additionally, I also estimated the net relatedness index (NRI) of the community. NRI was derived from observed and expected value and variance of mean pairwise distance (MPD) between all the species within each community. Expected value of MPD was generated by randomizing all the species within each savanna. This exercise was done for entire community and only for the native community. Two separate null models were used for each savanna. A mixed effect model was performed using various metric of functional diversity as response variable, savanna type and invasion gradient as fixed effect and each site as a random effect. An additional glmm was performed to test if remnant communities differ from uninvaded communities. The above analysis was performed in picante package in R (Kembel et al. 2020).

Phylogenetic diversity

I used the default megatree to construct the dated phylogenetic tree under the scenario 3 of all the species across the two savannas using the vphylomkaer2 in R (Jin and Qian 2022). For the 219

species in our dataset matches were found for 116 species, the remaining 105 were binned to the backbone using the general level polytomy. This tree was pruned for each savanna which was then used to measure the NRI of each community within the savanna. Standard effect size of phylogenetic MPD (Ses.mpd) was computed using both abundance weighted and unweighted approaches. The null model used shuffled the names of species 999 times across the tip of phylogenetic tree for each savanna using picante pacakge (Kembel et al. 2020). Ses.mpd was multiplied by -1 to generate net relatedness index (NRI) values for each community. This exercise was done for entire community and only for the native community. Further, to test if the phylogenetic distances are a good proxy for the function distances, I calculated unweighted pdNRI and fdNRI of communities using the dominant species. I performed a mixed effect model using NRI as response variable, savanna type and invasion gradient as fixed effect and each site as a random effect. An additional glmm was performed to test if remnant communities differ from uninvaded communities (Bates et al. 2023).

Beta Phylogenetic and functional diversity

To study the impact of invasion on phylogenetic and functional beta diversity at larger spatial scales, beta diversity for each invasion level within each site was estimated using beta.multi function in BAT package (Cardoso et al. 2015). Total functional and phylogenetic beta diversity along with its component (turnover and nestedness) was quantified. A mixed effect model was performed by, using dissimilarity metric (total beta, turnover and nestedness) as response variable, savanna type and invasion gradient as fixed effect and site as random effect. An additional glmm was performed to test if remnant communities differ from uninvaded communities.

Results

Community weighted trait means

To identify change in dominant trait composition of communities, changes in community weighted trait values for each trait across invasion gradient were analyzed. Traits associated with resource acquisition such as LMA, LDMC decreased whereas leaf nitrogen content increased with invasion in both savannas. Increase in leaf nitrogen content was more rapid in the FLS than in BLS. Traits associated with competition such as leaf area and height, also increased across the invasion gradient, in both savannas however the increase was more in FLS than in BLS (Figure 1). There was no difference in community weighted seed volume across invasion gradient in the two savannas. Native herbaceous communities in both savannas, behave similar to each other with invaded communities in both savannas having more resource acquisitive and competitive traits. The observed increase in stem diameter in FLS, disappears when only native herbaceous species were studied (Table 1; Appendix: Figure 1). Additionally, I found both Remnant and uninvaded communities had comparable trait composition (Appendix: Table 1).

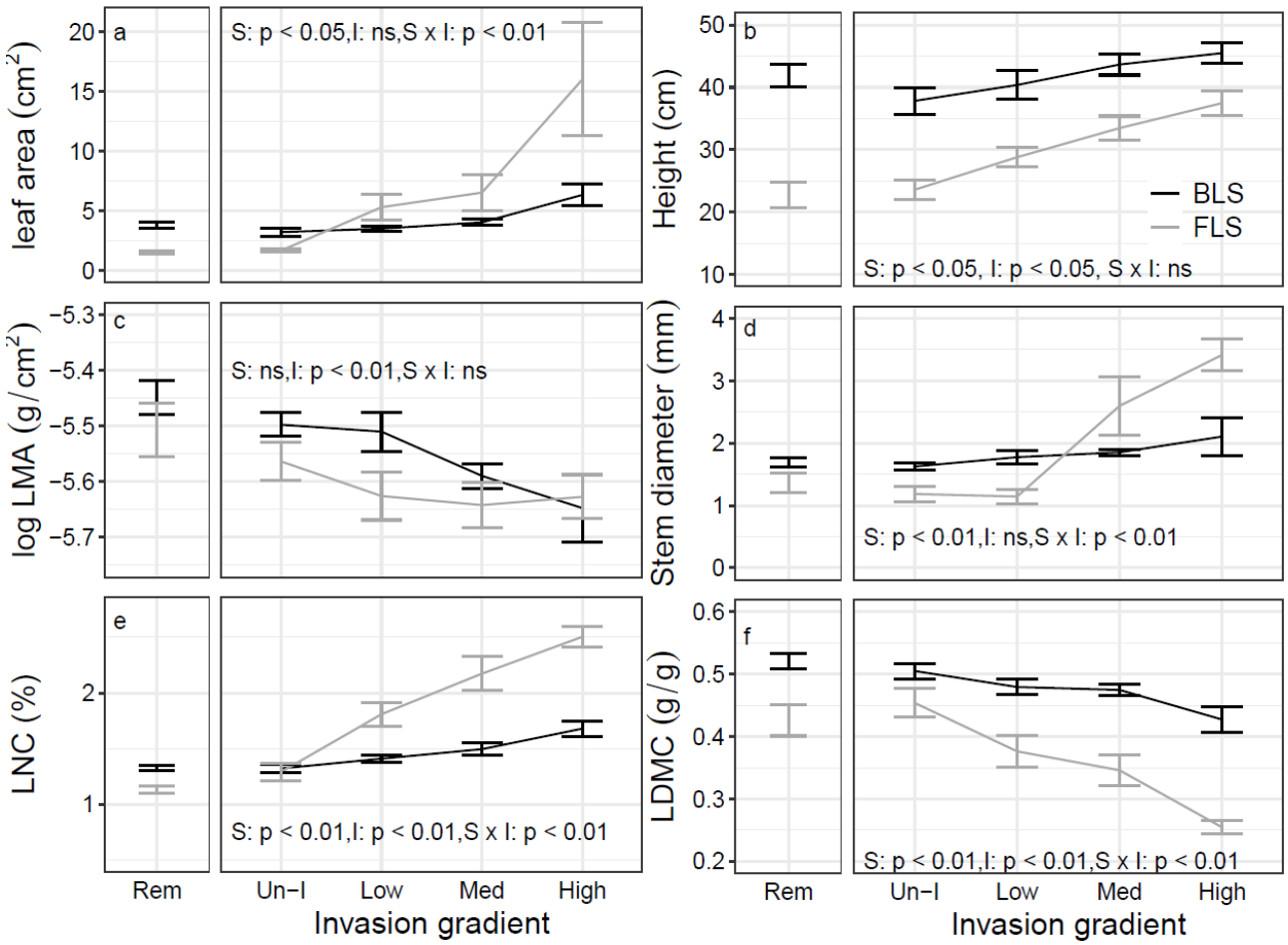

Figure 1: Community weighted trait means across invasion gradient in two savannas (black- BLS, gray- FLS). Community weighted means (± SE) of traits related to - competition a) leaf area; b) height; and, resource acquisition c) leaf mass per unit area; d) stem diameter; e) leaf nitrogen content; and, f) leaf dry matter content across invasion gradient. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

Table 1: Community weighted trait means of native and entire herbaceous community across invasion gradient in two savannas. Community weighted means of traits related to - competition a) leaf area; b) height; and, resource acquisition c) leaf mass per unit area; d) stem diameter; e) leaf nitrogen content; and, f) leaf dry matter content across invasion gradient. The results presented are p-values from type III Wald chi- square test for community weighted trait means with savanna and invasion gradient as fixed effects and site as a random effect

	Native herbaceous species			**All herbaceous species**		
Community weighted trait	**Savanna (S)**	**Invasion gradient (I)**	**S×I**	**Savanna (S)**	**Invasion gradient (I)**	**S×I**
a) Leaf area	<0.1	<0.01	ns	<0.05	ns	<0.01
b) Height	<0.1	<0.1	ns	<0.05	<0.05	ns
c) LMA	ns	<0.001	ns	ns	<0.01	ns
d) Stem diameter	ns	ns	ns	<0.01	ns	<0.01
e) LNC	ns	<0.05	ns	<0.01	<0.01	<0.01
f) LDMC	<0.1	<0.1	ns	<0.01	<0.01	<0.01

When shift in the multivariate trait space of communities across invasion gradient, were studied, I found significant differences in trait composition across invasion gradient in two savannas (Appendix: Table 2). Invaded communities were found to be more resource acquisitive and competitive in both savannas. In BLS, community weighted nitrogen content increased primarily in the direction of invasion. On the other hand in FLS invaded communities had both higher resource acquisitive (LDMC and LMA) and competitive traits (LA) (Figure 2). However, when only native herbaceous community were analyzed, I found that native species in invaded communities were more resource acquisitive in both savannas (Appendix: Figure 2, Table 3).

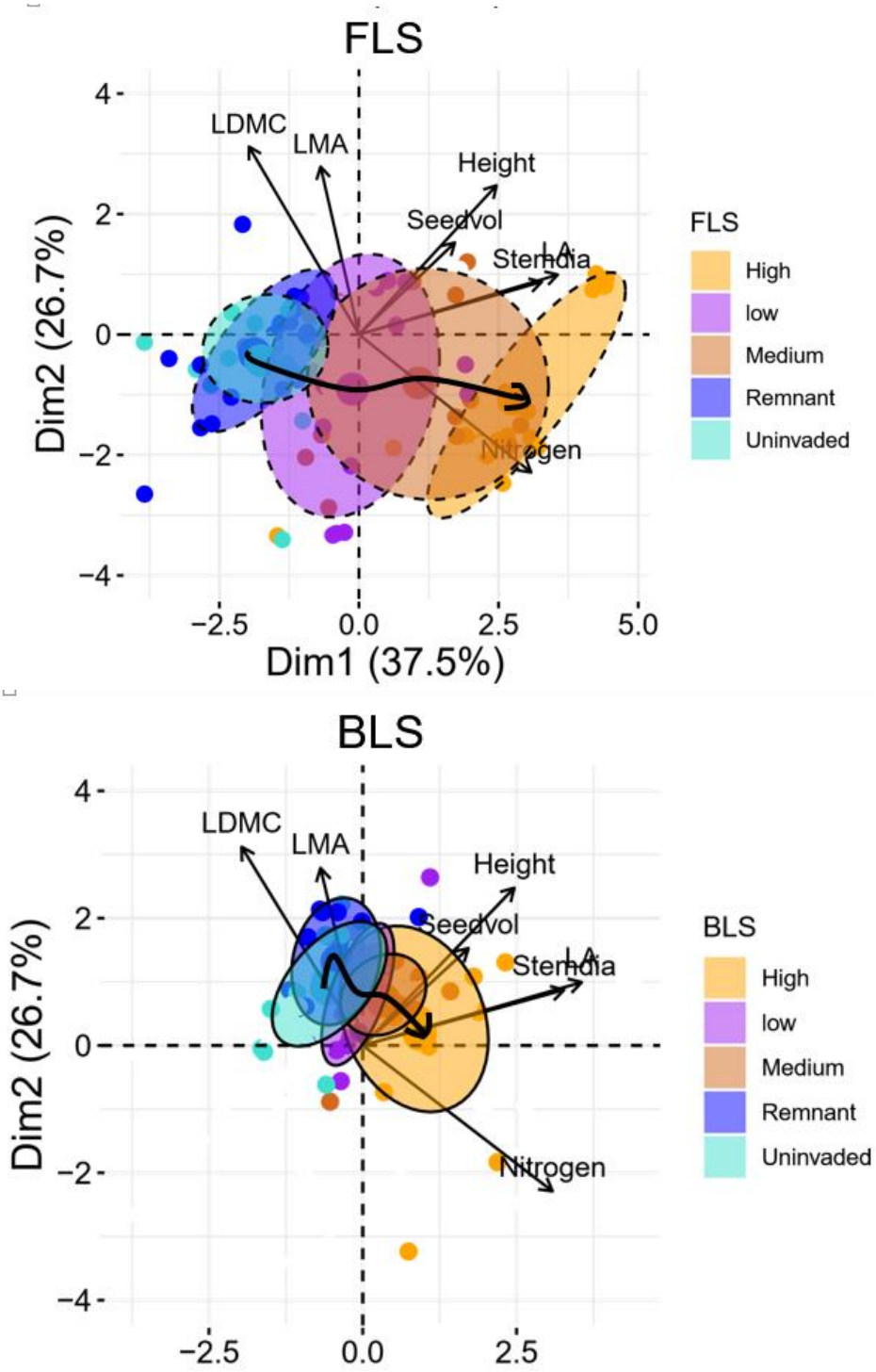

Figure 2: Change in community weighted mean for multiple traits across invasion gradient. Principal component analysis of community weighted traits associated with competition (LA, height), resource acquisition (LMA, LDMC, nitrogen) and reproductive ability (seed volume). The figure shows first two PC axis for changes across invasion gradient in fine leaf savanna (FLS) and broad leaf savanna (BLS). Ellipses represent 95% SE.

Functional diversity

To measure the functional diversity I quantified three major components of functional diversity: functional richness, functional evenness and functional divergence. Functional richness measured using the FD metric measures the trait ranges of species in multidimensional trait space. Functional richness is correlated with taxonomic richness (Appendix: Figure 3), therefore I also measured net relatedness index which is independent of species richness (Appendix: Figure 3). In both savannas, increase in invasion was associated with increase in community functional richness. There was however, no difference in the functional evenness across invasion gradient. Interestingly I found that, communities in FLS, became more divergent with increase in invasion, but in BLS divergence did not change with increasing invasion (Figure 3). When only native species were considered, no significant differences were found in functional richness, evenness and divergence for both savannas, but NRI-FD increased with invasion in BLS (Table 2, Appendix: Figure 4). Additionally, when woody species were also used to measure functional richness I found functional richness increased with invasion in both savannas (Appendix: Figure 5, 6). Interestingly, Remnant and uninvaded herbaceous communities differ in their functional divergence in the two savannas (Appendix: Table 4, 5).

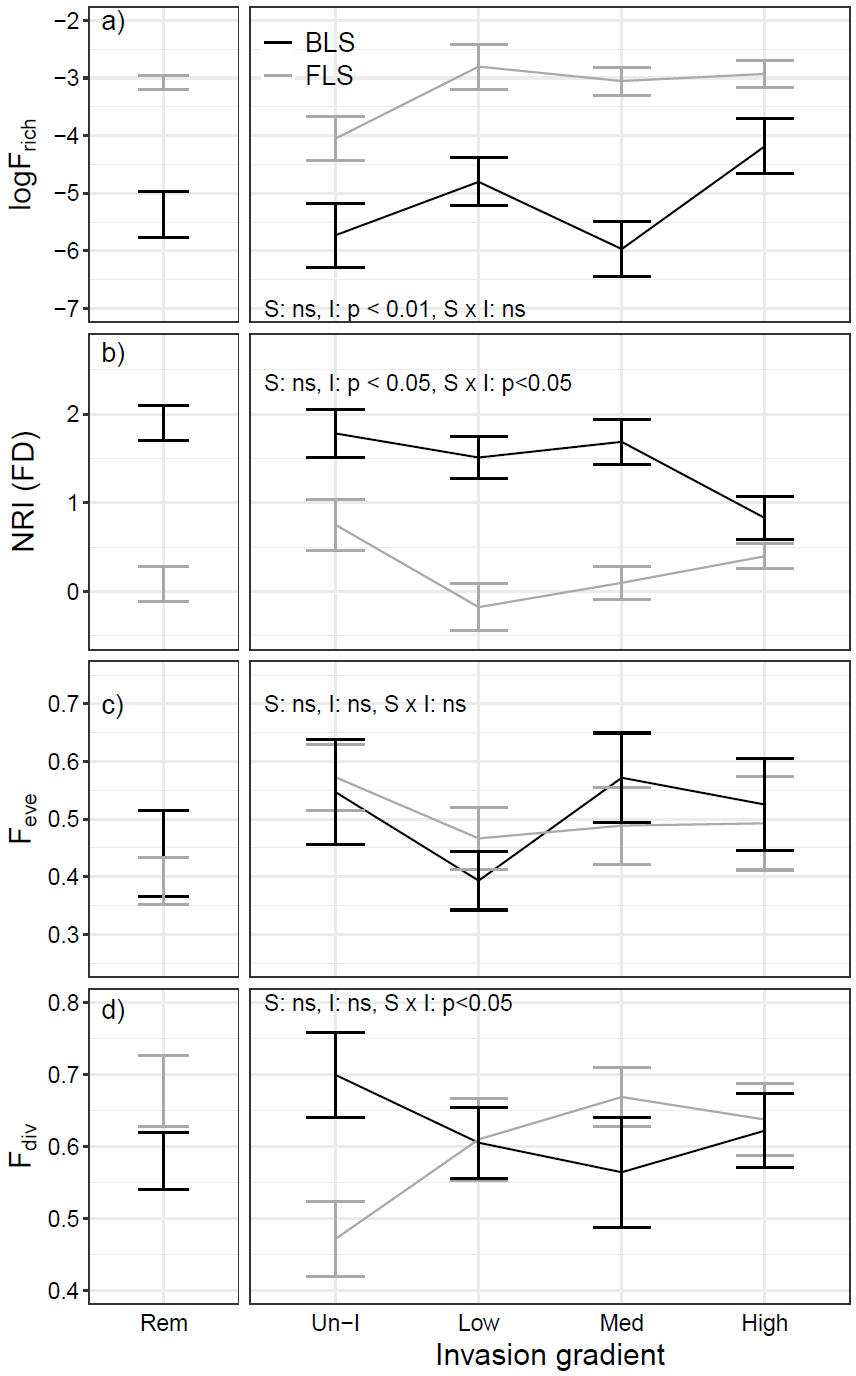

Figure 3: Change in functional diversity across invasion gradient in two savannas (black- BLS, gray- FLS). Mean and SE for various metric of functional diversity measured for two savannas a) functional richness; b) net relatedness index; c) functional evenness; and, d) functional divergence. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction

Table 2: Change in functional diversity of native and entire herbaceous community across invasion gradient in two savannas. Different metric of functional diversity measured for two savannas a) functional richness; b) net relatedness index; c) functional evenness; and, d) functional divergence. The results presented are p-values from type III Wald chi- square test for diversity measures with savanna and invasion gradient as fixed effects and site as a random effect

	Native herbaceous species			**All herbaceous species**		
Functional diversty	**Savanna (S)**	**Invasion gradient (I)**	**S×I**	**Savanna (S)**	**Invasion gradient (I)**	**S×I**
a) F_{rich}	ns	ns	ns	ns	<0.01	ns
b) NRI-FD	ns	ns	<0.05	ns	<0.05	<0.05
c) F_{eve}	ns	ns	ns	ns	ns	ns
d) F_{div}	ns	ns	<0.1	ns	ns	<0.05

Relationship between FD and PD for dominant herbaceous species

Functional diversity and phylogenetic diversity was measured as net relatedness index (NRI) for all the dominant herbaceous species found in the two savannas. NRI for both phylogenetic distance and functional distance were correlated (r 0.7, p <0.001), for both savannas (Figure 4). Such strong co-relation points towards phylogenetic diversity (NRI-PD) being a good proxy for functional diversity (NRI-FD) in these systems.

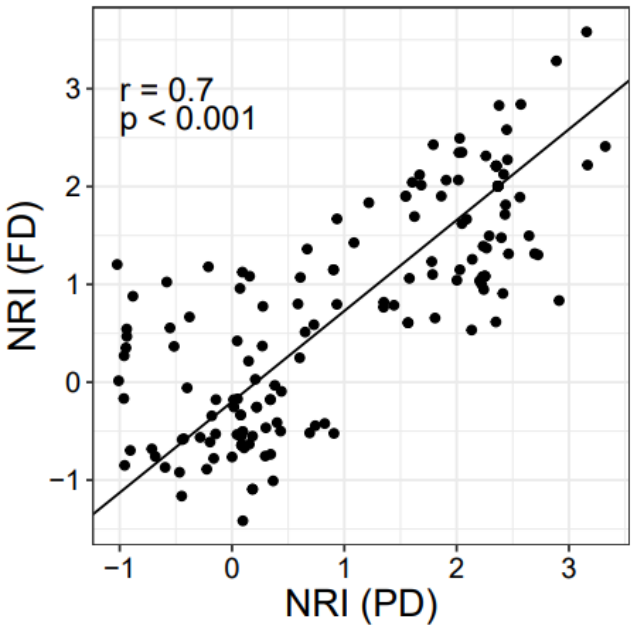

Figure 4: Correlation between net relatedness index of functional (NRI-FD) and phylogenetic distances (NRI-PD) between species in both savannas. Each point represents the 10x10m plot across invasion gradient in both savannas. The line is the type 2 regression fit.

Phylogenetic diversity

Phylogenetic diversity measured as net relatedness index amongst herbaceous species showed a decline with increasing invasion in both savannas (Figure 5). For native herbaceous communities, opposite trends were seen across gradient in the two savannas, with NRI-PD increasing in FLS and decreasing in BLS with invasion (Appendix: Figure 7). Additionally, when PD was estimated by incorporating woody species I found decrease in NRI-PD for BLS, whereas when only native communities were studied (woody included) but no change in NRI-PD was observed across invasion gradient (Appendix: Figure 8). Interestingly, Remnant and uninvaded communities differ in their phylogenetic diversity in the two savannas (Appendix: Table 6).

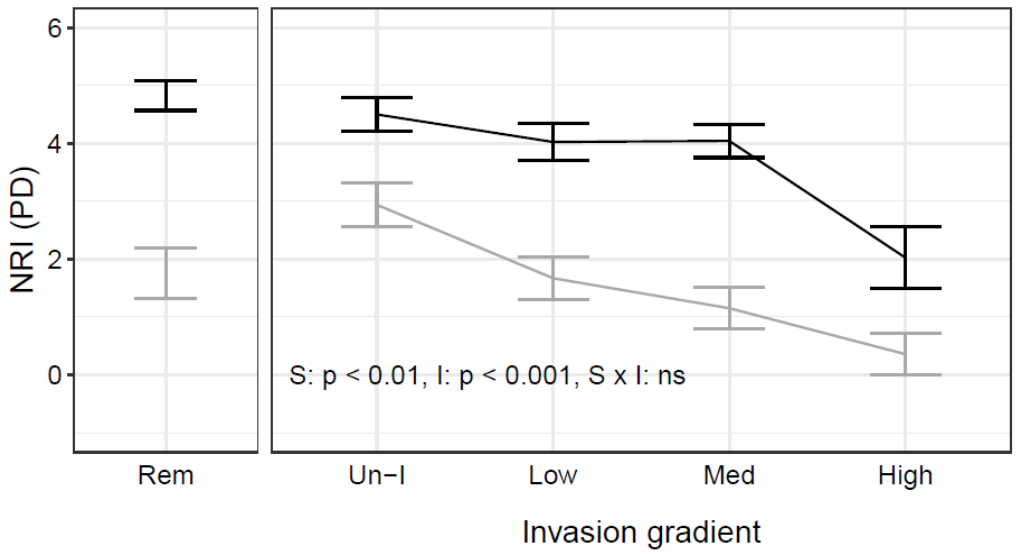

Figure 5: Phylogenetic net relatedness index (NRI) of communities across invasion gradient. The values are mean± SE of abundance weighted NRI for herbaceous community. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species.

Beta Phylogenetic and functional diversity

Functional beta diversity increased across invasion gradient in BLS but decreased in FLS (Figure 6a), whereas phylogenetic beta diversity increased in both savannas (Figure 7a). Further, when underlying components of total beta diversity were analyzed, I found that turnover contributed more than nestedness to the observed overall phylogenetic and functional beta diversity (Figure 6, 7). Functional turnover decreased in FLS, but there was no difference in functional turnover in BLS (Figure 6b). Phylogenetic turnover was highest in moderately invaded communities in both savannas (Figure 7b). Finally, phylogenetic nestedness increased with invasion in both savannas but there was no significant difference in functional nestedness (Figure 6c, 7c). There was no significant difference between remnant and uninvaded communities in functional, phylogenetic beta diversity and its components. Overall I find that phylogenetic and functional beta diversity

behave similar to taxonomic beta diversity that is at larger spatial scales, invaded communities are more heterogeneous than uninvaded communities.

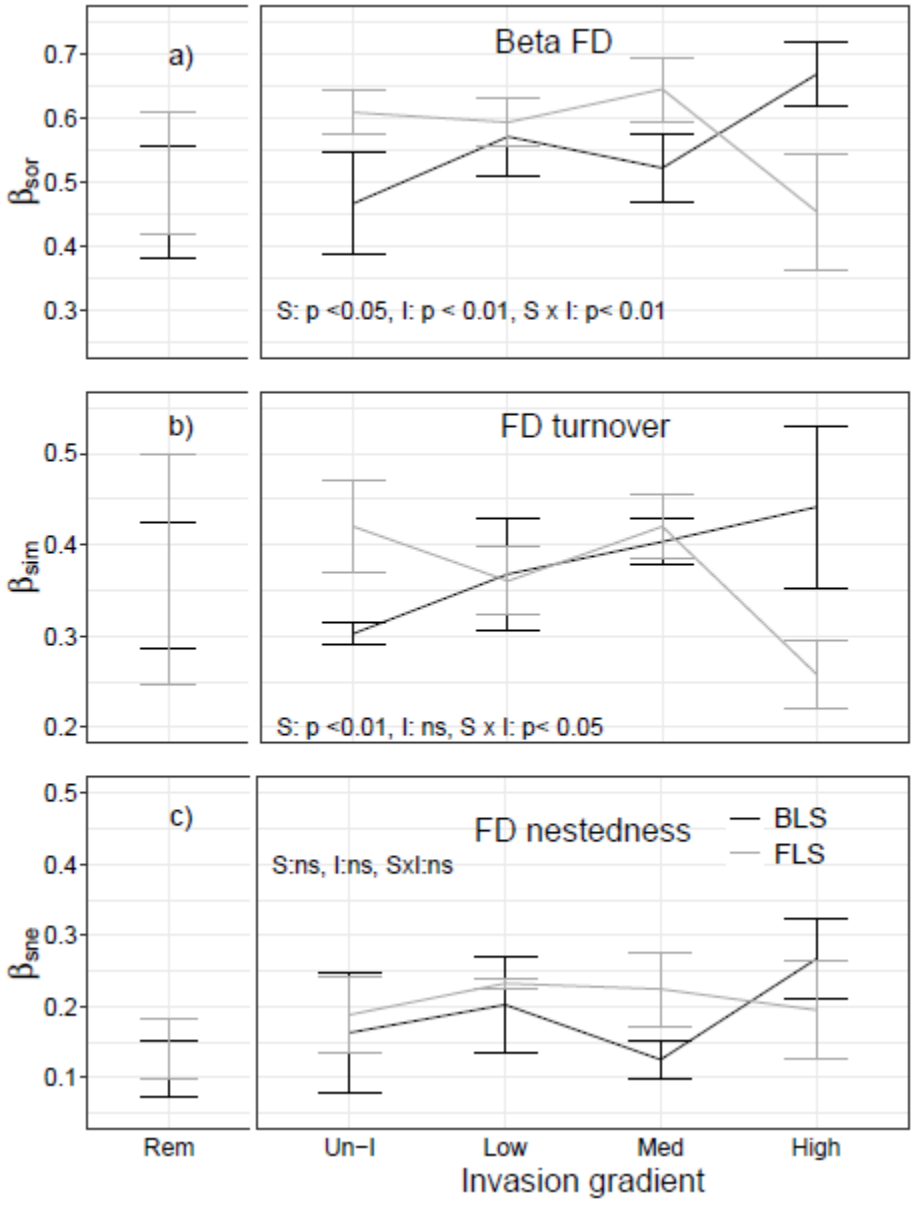

Figure 6: Functional beta diversity and its components of herbaceous community across invasion gradient in two savannas (Black-BLS, gray-FLS). Mean ± SE for a) total functional beta diversity; b) turnover; and, c) nestedness. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction

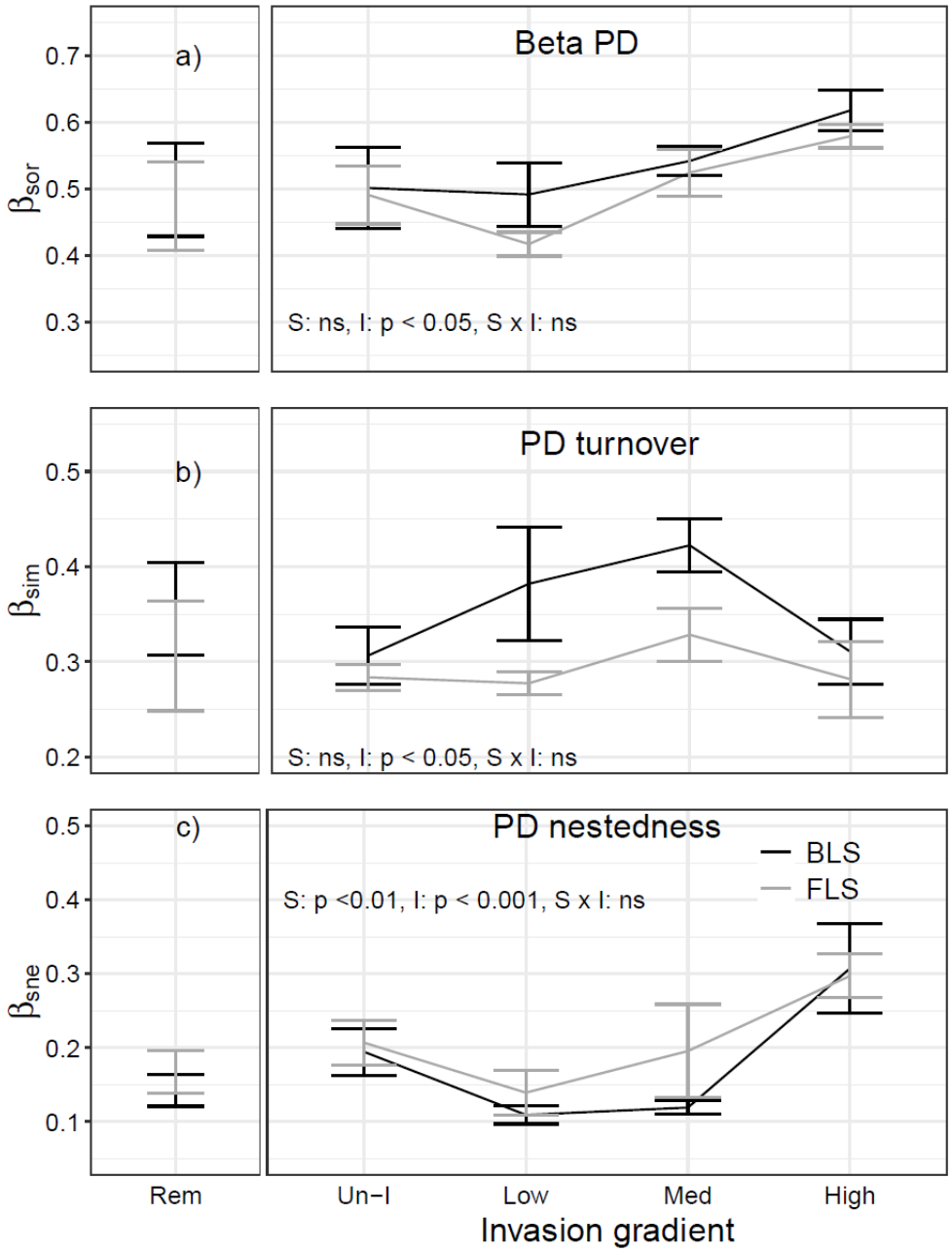

Figure 7: Phylogenetic beta diversity and its components of herbaceous community across invasion gradient in two savannas (Black-BLS, gray-FLS). Mean ± SE for a) total phylogenetic beta diversity; b) turnover; and, c) nestedness. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction

Discussion

In this chapter, I studied the impact of invasion on functional and phylogenetic composition of herbaceous savanna communities. To understand the shift in dominant trait strategy and functional diversity, I studied the changes in community weighted trait means and various metric of functional and phylogenetic diversity across invasion gradient in two savannas. The results show that as per the expectations, invaded communities in savannas have traits corresponding to rapid resource acquisition and higher competitive ability. They also have higher functional richness, primarily being driven by invader which is functionally different from the native community. I also show that in both of these savannas phylogenetic diversity is a good proxy for functional diversity. Therefore in the absence of functional data, phylogenetic information which are more readily available can be used to understand both the mechanism and impact of invasion in these systems.

Overall results suggests that invaded communities in both savannas have more competitive and resource acquisitive strategy. Community weighted mean values of leaf area, height, stem diameter and LNC increased, whereas LDMC and LMA decreased across invasion gradient. Although invaded communities differ across all traits, the primary difference was along traits associated with competitive ability (height and LA) and resource acquisition (LNC, LMA). There changes are more prominent in FLS than in the BLS, however this was because trait of invader in FLS being herbaceous was included in analysis but in BLS invader traits were omitted as invader was of woody lifeform. To control for this, I only considered changes in traits of native communities. As expected I found comparable changes with invasion across both savannas. Native species in invaded communities were taller and had lower LDMC than native

communities in uninvaded plots. Higher competitive and resource acquisitive strategy of native species in invaded communities can be caused when invaders selectively replace slow growing natives. An alternate reason can be the presence of high disturbance in these savannas (Gadgil and Malthotra 1982). Disturbance can alter resource availability in community such that only fast growing natives or invasive species can persist under the altered disturbance regime (Grime 1974). Furthermore, invasive species in invaded regions are taller and have higher LDMC than co-occurring natives. Our results are similar to (Sodhi et al. 2019; Hejda and Bello 2013) which showed that invaders are functionally different from natives and lead to shift in optimal height and LDMC of the community.

Functional diversity of a community can increase if it is invaded by a species which is very dissimilar to the co-occurring native. Our results show that invaded communities in both savannas are functionally richer that uninvaded communities. However, no difference in the functional richness was found between the native communities across the invasion gradient. This shows that it is the functionally distinct invaders in these savannas which are leading to higher functional richness of invaded communities, corroborating with the law of limiting similarity (Hutchinson 1959) .This was further supported by higher functional divergence of invaded communities, pointing towards invader possibly using niche expansion over niche filling to invade these savannas (Villéger et al. 2008). Although invaded communities had higher functional richness, no change was observed in functional evenness of communities. This was because for the FD measurements, I considered all those species which formed 90% community cover (Forey et al. 2023). Since, native communities in these savannas are composed of a few equally dominant species, the distribution of abundance along these traits in uninvaded

communities were similar to that of invaded communities, where a few invasive species co-dominated.

To understand the functional diversity one often need to collect trait data across multiple traits for the entire community. As this is often laborious in species rich ecosystems, ecologists either use only the dominant species (Forey et al. 2023) or use phylogenetic diversity of entire community as a proxy for functional diversity (Cadotte et al. 2019). Both the techniques can have drawbacks – a) dominant species need not give true representation of overall community diversity b) PD and FD can be decoupled due to differences in evolutionary rates of traits (Cadotte et al. 2019). However, our results show that in these savannas both PD and FD of the dominant species are correlated. Furthermore, FD of the community formed of dominant species and abundance weighted PD incorporating all the species also give similar results. Phylogenetic diversity measured as net relatedness index, shows that invaded communities become more phylogenetically dissimilar. Moreover, including invader increases the phylogenetic diversity of communities in both savannas. This is similar to the changes in functional richness measured using a subset of dominant species.

At larger spatial scale invaded communities are more heterogeneous compared to uninvaded communities in both savannas. Both phylogenetic and functional beta diversity patterns were similar to changes in taxonomic beta diversity across invasion gradient. This indicates that uninvaded communities have same set of common species or species which are phylogenetically similar to each other. On the other hand invaded systems are composed of different species

which are phylogenetically distinct from one another (Dyderski and Jagodziński 2021). Additionally, both functional and phylogenetic beta diversity is driven by turnover. This suggests that invaded communities host different set of species rather than presence of certain core species. Finally, high nestedness of highly invaded communities in both savannas may indicate selective extinction, making some functional groups to become more common (Dyderski and Jagodziński 2021).

The results from this chapter show that savannas in this region are invaded by species which are functionally dissimilar to the native communities. Different metric of functional and phylogenetic diversity show that invaded communities differ from uninvaded communities and these differences are being driven by invasive species. Although phylogenetic diversity is a good proxy for functional diversity in these systems, having functional traits gives more mechanistic insights into the impact of invasion. For example, the results show that invaded communities differ from uninvaded along traits associated with faster resource use and high competitive strategies. Such changes can alter nutrient cycling in the invaded savannas. Finally, I show that similar to taxonomic beta diversity, invasion at larger spatial scale leads to increase in community heterogeneity, caused by phylogenetic and functional turnover.

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Appendix:

Tables

Figures

Figure 1: Community weighted trait means of native herbaceous community across invasion gradient in two savannas (black- BLS, gray- FLS). Community weighted means (± SE) of traits related to - competition a) leaf area; b) height; and, resource acquisition c) leaf mass per unit area; d) stem diameter; e) leaf nitrogen content; and, f) leaf dry matter content across invasion gradient. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

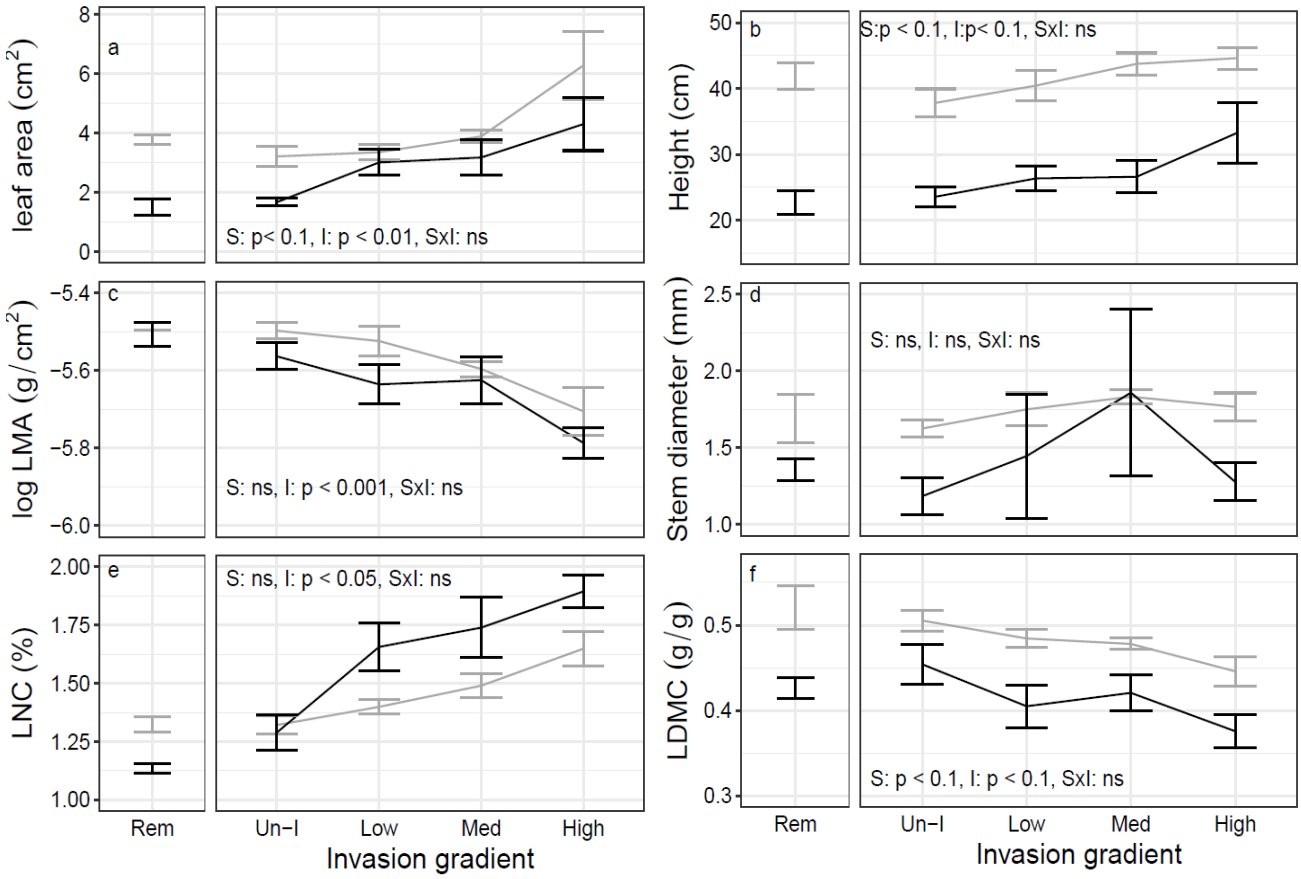

Table 1: Community weighted trait means of Remnant and Uninvaded herbaceous communities in two savannas. Community weighted means of traits related to - competition a) leaf area; b) height; and, resource acquisition c) leaf mass per unit area; d) stem diameter; e) leaf nitrogen content; and, f) leaf dry matter content across invasion gradient. The results presented are p-values from type III Wald chi- square test for community weighted trait means with savanna and remnant/uninvaded communities as fixed effects and site as a random effect

Community weighted trait	**Savanna (S)**	**Plot (P)**	**S×P**
a) Leaf area	<0.001	<0.1	<0.1
b) Height	<0.001	ns	ns
c) LMA	ns	ns	ns
d) Stem diameter	<0.05	ns	ns
e) LNC	<0.001	ns	<0.1
f) LDMC	<0.05	ns	ns

Table 2: Multidimensional community weighted trait means for entire herbaceous community across invasion gradient in two savannas. The results presented are of PERMANOVA model for community weighted traits with savanna type and invasion gradient as fixed effects

Effects	***df***	**SS**	**r^2**	***F***	***p* value**
Savanna	1	119.10	0.11	27.28	0.001
Invasion gradient	4	241.61	0.22	13.83	0.001
Savanna x Invasion gradient	4	81.73	0.07	4.68	0.001
Residual	144	628.56	0.58		
Total	153	1071.00	1		

Table 3: Multidimensional community weighted trait means for native herbaceous community across invasion gradient in two savannas. The results presented are of PERMANOVA model for community weighted traits with savanna type and invasion gradient as fixed effects

Effects	***df***	**SS**	**r^2**	***F***	***p* value**
Savanna	1	160.09	0.14	31.02	0.001
Invasion gradient	4	146.79	0.13	7.11	0.001
Savanna x Invasion gradient	4	24.67	0.02	1.19	0.237
Residual	146	753.45	0.69		
Total	155	1085.00	1		

Figure 2: Change in community weighted mean for multiple traits of native herbaceous community across invasion gradient. Principal component analysis of community weighted traits associated with competition (LA, height), resource acquisition (LMA, LDMC, nitrogen) and reproductive ability (seed volume). The figure shows first two PC axis for changes across invasion gradient in fine leaf savanna (FLS) and broad leaf savanna (BLS). Ellipses represent 95% SE.

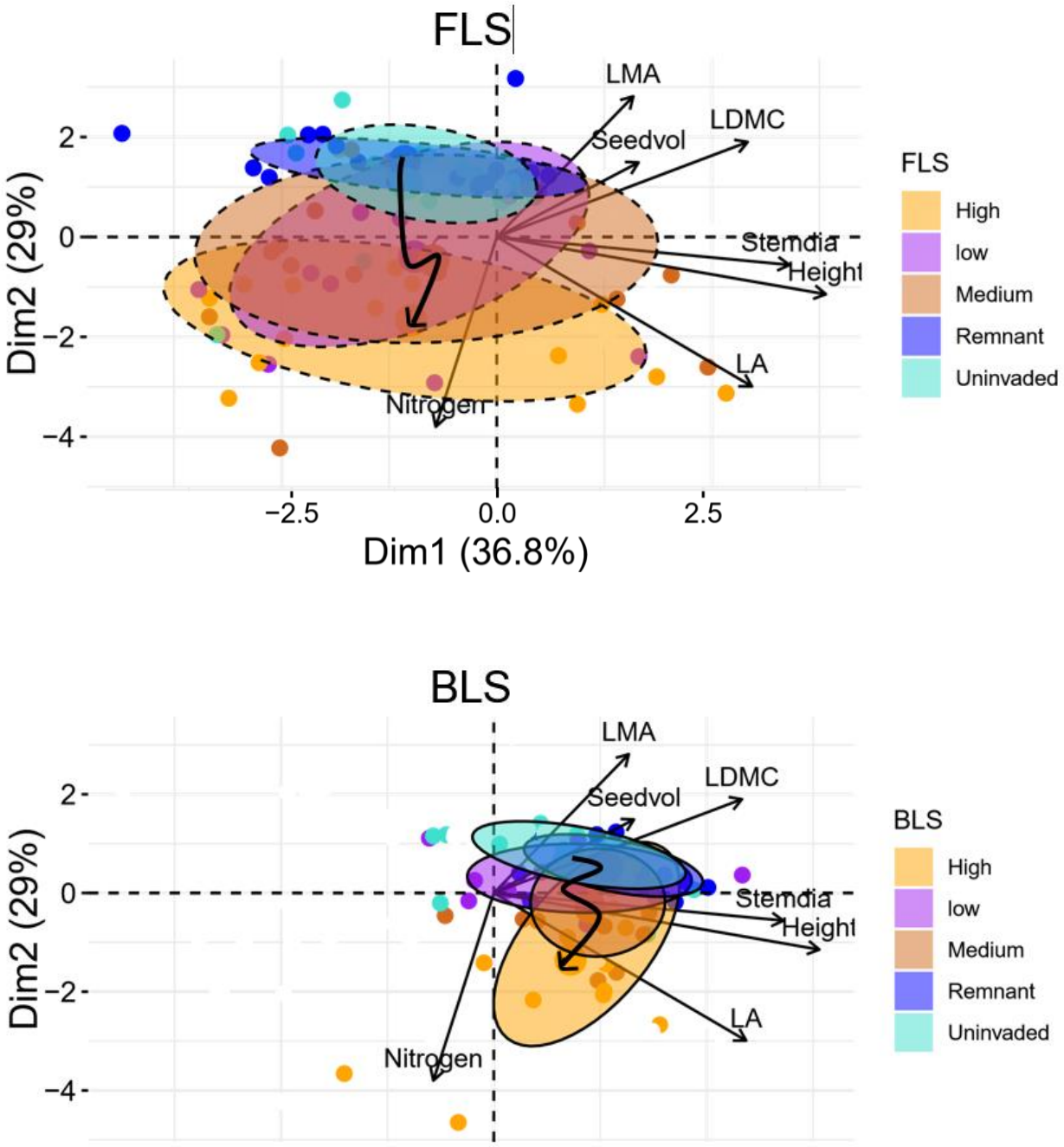

Figure 3: Relationship between Species richness within a plot with two measures of functional richness a) Frich; and, b) Net relatedness index (NRI).

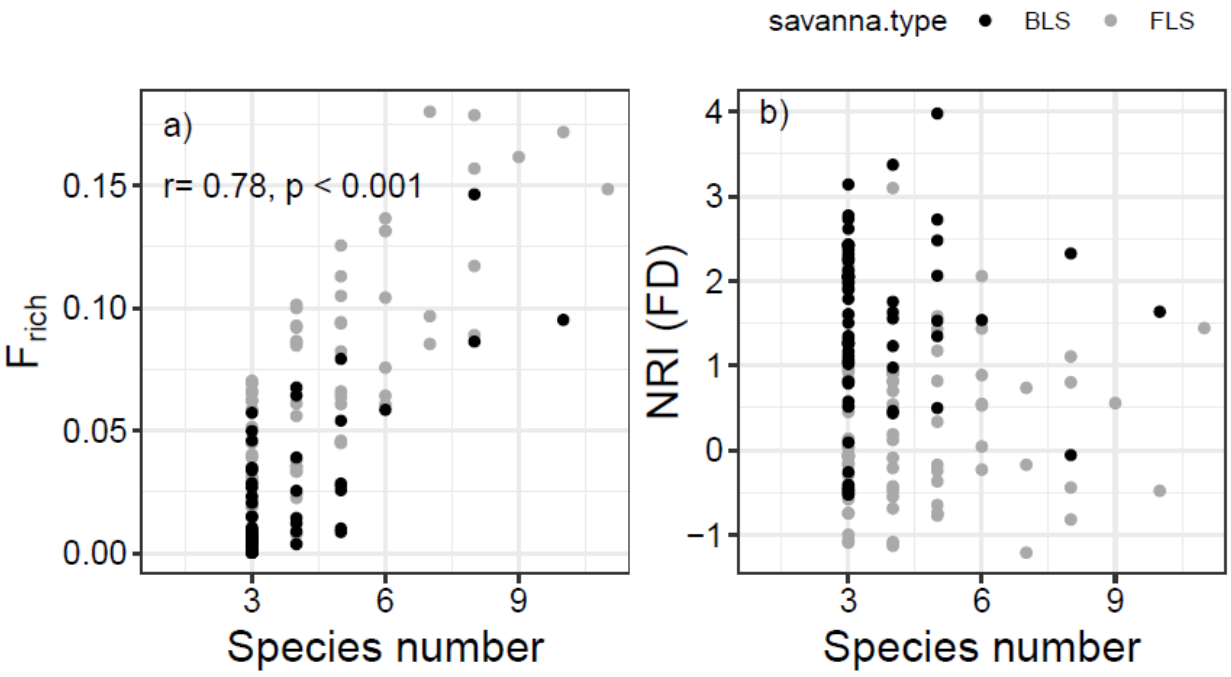

Figure 4: Change in functional diversity of native herbaceous communities across invasion gradient in two savannas (black- BLS, gray- FLS). Mean and SE for various metric of functional diversity measured for two savannas a) functional richness; b) net relatedness index; c) functional evenness; and, d) functional divergence. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction.

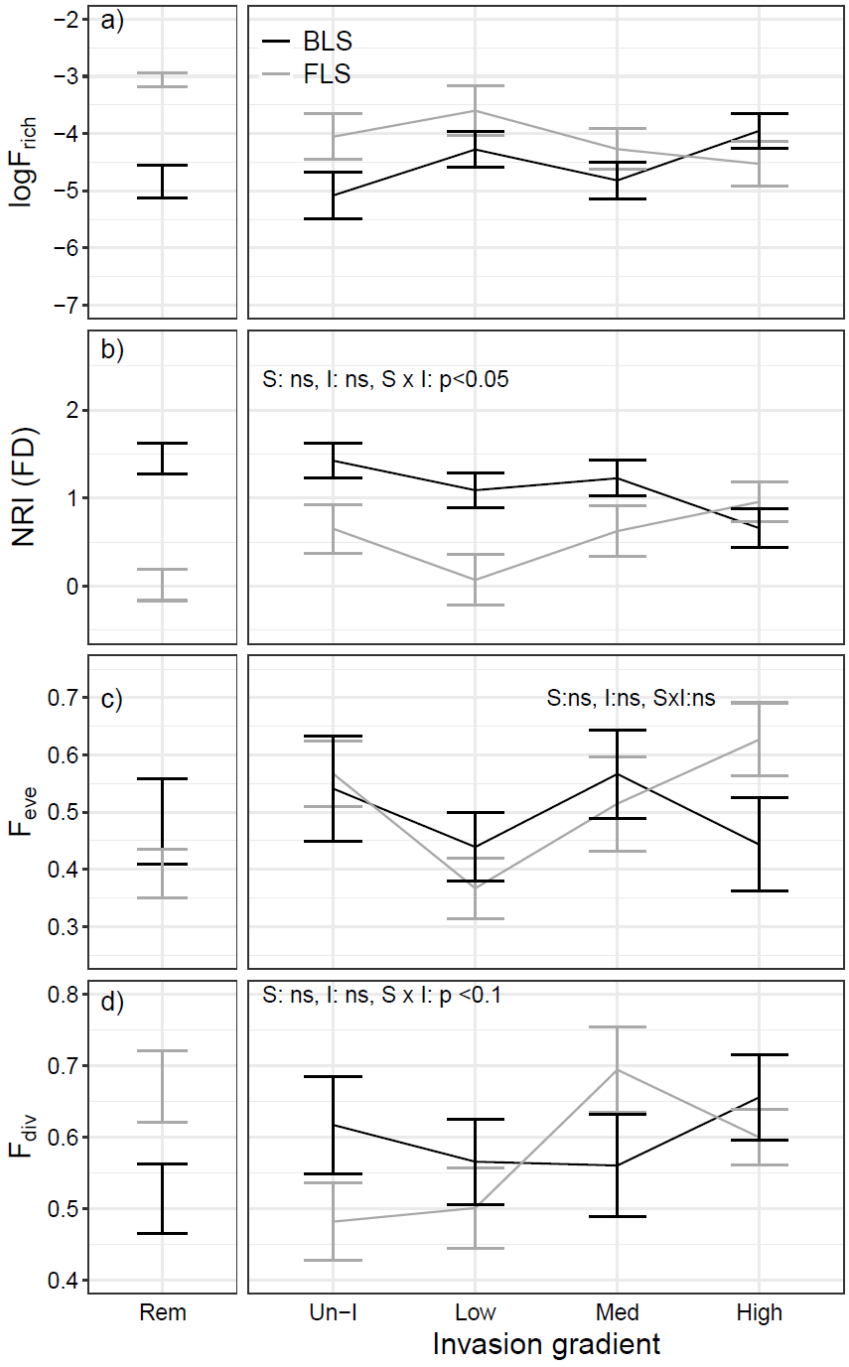

Figure 5: Change in functional richness of community (woody included) across invasion gradient in two savannas (black- BLS, gray- FLS). Mean and SE for a) functional richness for entire community; b) functional richness native community (woody natives included) measured for two savannas. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction

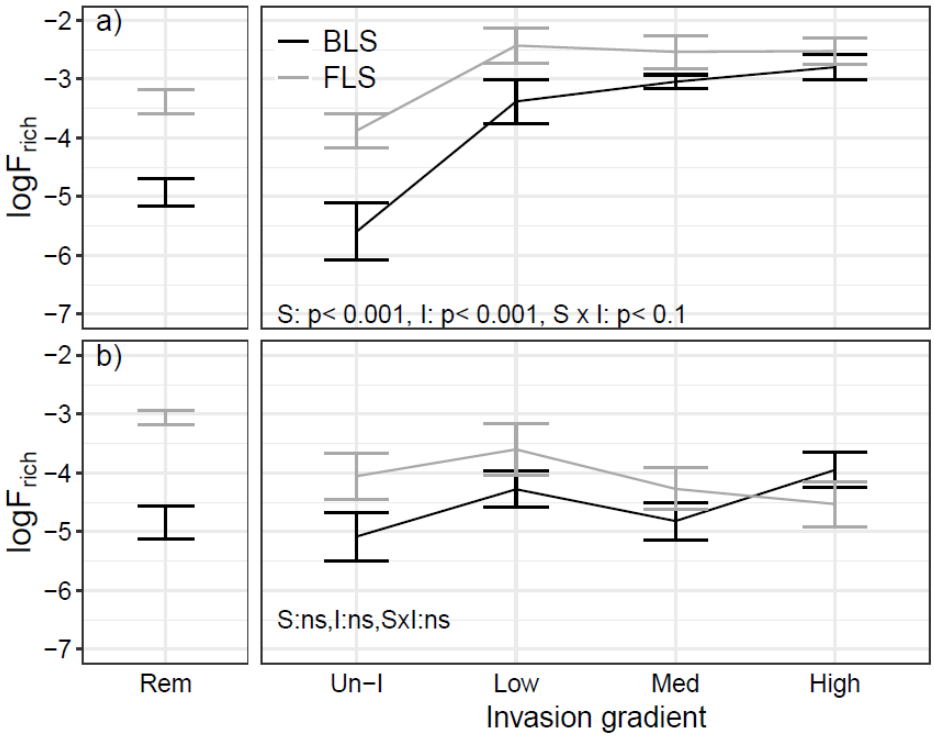

Figure 6: Change in functional richness of community (woody included) across invasion gradient in two savannas (black- BLS, gray- FLS). Mean and SE for a) net relatedness index for entire community; and, b) net relatedness index native community (woody natives included) measured for two savannas. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. P-values for the statistical tests are presented with 'ns' denoting not significant at $p < 0.1$. S - Savanna type; I - invasion gradient; S × I - Savanna type and Invasion gradient interaction

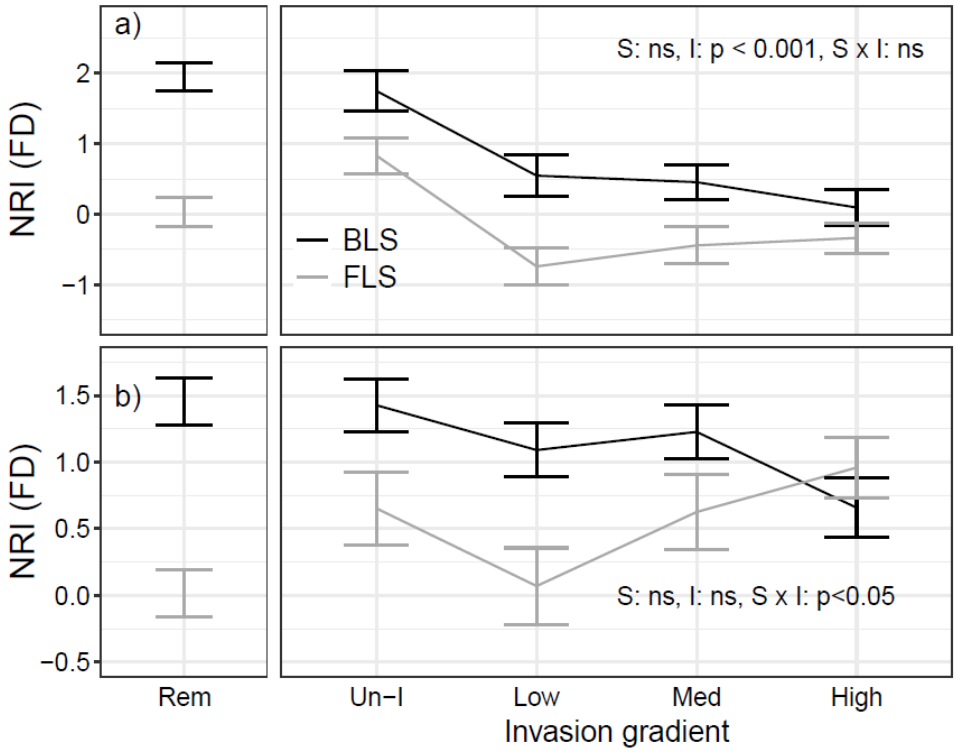

Table 4: Change in functional diversity of Remnant and uninvaded herbaceous community in two savannas. Different metric of functional diversity measured for two savannas a) functional richness; b) net relatedness index; c) functional evenness; and, d) functional divergence. The results presented are p-values from type III Wald chi- square test for diversity measures with savanna and remnant/uninvaded communities as fixed effects and site as a random effect

Functional diversity	**Savanna (S)**	**Plot (P)**	**S × P**
a) F_{rich}	<0.01	ns	ns
b) NRI-FD	<0.001	ns	<0.1
c) F_{eve}	ns	ns	ns
d) F_{div}	ns	<0.1	<0.001

Table 5: Change in functional diversity of Remnant and uninvaded communities (woody included) in two savannas. Different metric of functional diversity measured for two savannas a) functional richness; and, b) net relatedness index. The results presented are p-values from type III Wald chi- square test for diversity measures with savanna and remnant/uninvaded communities as fixed effects and site as a random effect

Functional diversity	**Savanna (S)**	**Plot (P)**	**S × P**
a) F_{rich}	<0.001	ns	ns
b) NRI-FD	<0.001	ns	<0.05

Figure 7: Phylogenetic net relatedness index (NRI) of native herbaceous communities across invasion gradient. The values are mean± SE of abundance weighted NRI for herbaceous community. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species.

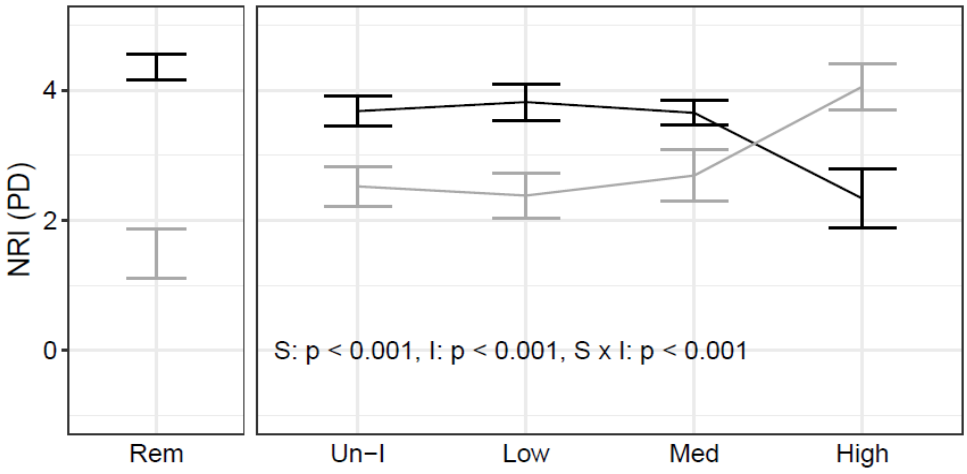

Figure 8: Phylogenetic net relatedness index (NRI) of entire community (woody included) across invasion gradient. The values are mean± SE of a) unweighted NRI for entire community (woody included); and, b) native community (native woody included). Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species.

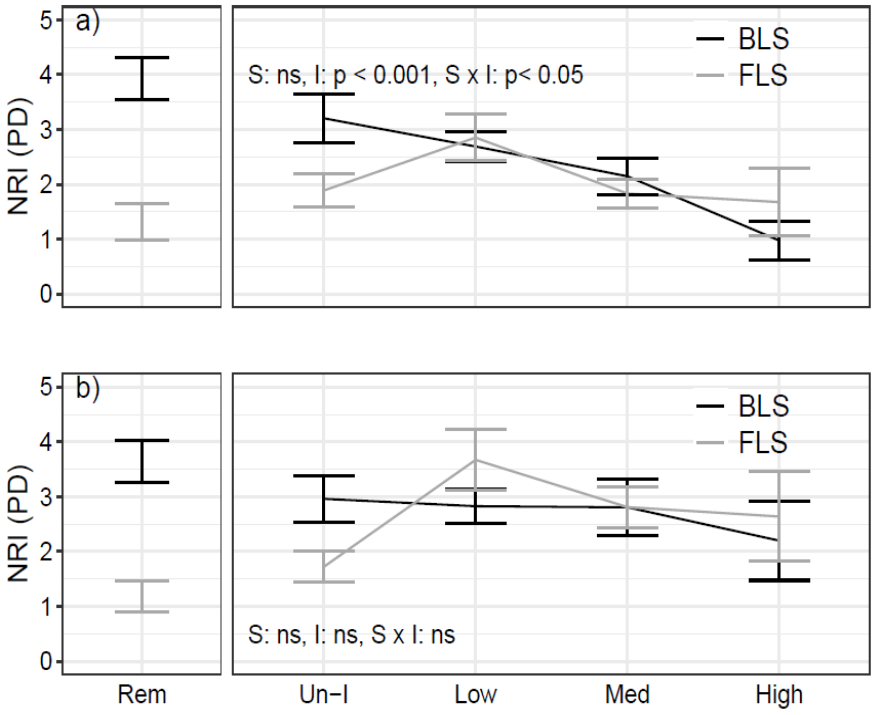

Table 6: Change in phylogenetic diversity of remnant and uninvaded communities in two savannas. Phylogenetic diversity measured as NRI-PD for two savannas a) herbaceous species only; and, b) entire community (woody included). The results presented are p-values from type III Wald chi- square test for diversity measures with savanna and remnant/uninvaded communities as fixed effects and site as a random effect

Community weighted Trait	**Savanna (S)**	**Plot (P)**	**S × P**
a) NRI-PD herb	<0.001	ns	<0.001
b) NRI-PD all	<0.001	ns	<0.05

Chapter 6: Conclusions

This thesis, identifies and characterizes major invasive plants of the Northern Western Ghats and Konkan regions (NWGK). This is a first comprehensive study on invasive plants from this region. It provides a prioritized list of invasive plants which can inform the decisions of landscape managers and restoration practitioners for management of invasive plants in this region (Chapter 2). Furthermore, trait based approach has been used to characterize these invasive species. I identified the relationship between functional traits and invasion success in NWGK. This characterization is important for risk assessment of future invasion in this region (Chapter 3). Finally, this study reveals the differential impact of invasion in two types of savannas at multiple spatial scale. The results from this study show that broad leaf savannas are more negatively impacted by invasion than fine leaved savannas. To the best of my knowledge, no study till date has assessed the impact of invasion on taxonomic, functional and phylogenetic diversity in Asian tropical savannas (Chapter 4, 5).

To begin with in Chapter 2, a major knowledge gap was filled, by identifying the major invasive plants of NWGK and study their spatial distribution in the region. In this chapter, two complementary approaches were used to get comprehensive understanding of various demographic and impact dimensions of invasive plants. Herbaria and floras were used to understand range size and temporal dynamics of species and expert knowledge provided information on other demographic dimensions such as local abundance and impact dimensions of these species. This exercise helped in generating a prioritized list of invasive plants, with six species having high priority scores. Furthermore, in chapter 3, these species were characterized

based on their functional traits. Resource acquisitive traits such as LDMC and ruderal strategies were associated with successful invasion in this region. In Chapter 4, I estimated impact of invasion gradient at two different spatial scales in savannas found on eastern edge of the NWGK. Broad leaf savannas (BLS) were more negatively impacted by invasion than fine leaf savanna (FLS). Interestingly, in both the savannas invaded communities were more heterogeneous than uninvaded communities. This suggests that in these systems impact of invasion at smaller spatial scales must not be linearly translated to impact at larger spatial scales.

Finally, in chapter 5, I see that changes observed in community composition as shown in chapter 4, leads to alteration in dominant trait of invaded communities. Invaded communities had ecological strategies associated with faster resource use and high competition. Changes in community weighted means of these traits are driven by changes in taxonomic community composition. Uninvaded systems have traits similar to indicator old growth savanna species, whereas invaded community weighted traits are being driven by invasive species found in these regions (Figure 1). Since invasive species occupy a distinct trait space than native species (Chapter 3), as expected this lead to an increase in functional and phylogenetic diversity. I also found that differences in taxonomic diversity is also reflected functional and phylogenetic diversity at larger spatial scales i.e beta diversity. I showed that invaded communities in both savannas had higher beta diversity as they were more taxonomically and phylogenetically heterogeneous than uninvaded communities. Overall, our results showed that invasion causes changes in taxonomic, functional and phylogenetic diversity of savannas located in the eastern edge of Western Ghats. Overall in this thesis I show that invasive plants of NWGK are widespread and a few of them have high impact across various dimensions and should be

managed on priority. Species with resource acquisitive traits have higher potential of being successful and therefore during introduction species with such trait combinations must be screened. Finally, invasion causes alteration in taxonomic, functional and phylogenetic diversity of savannas but these impacts are differentially higher in BLS which are already rapidly declining in this region.

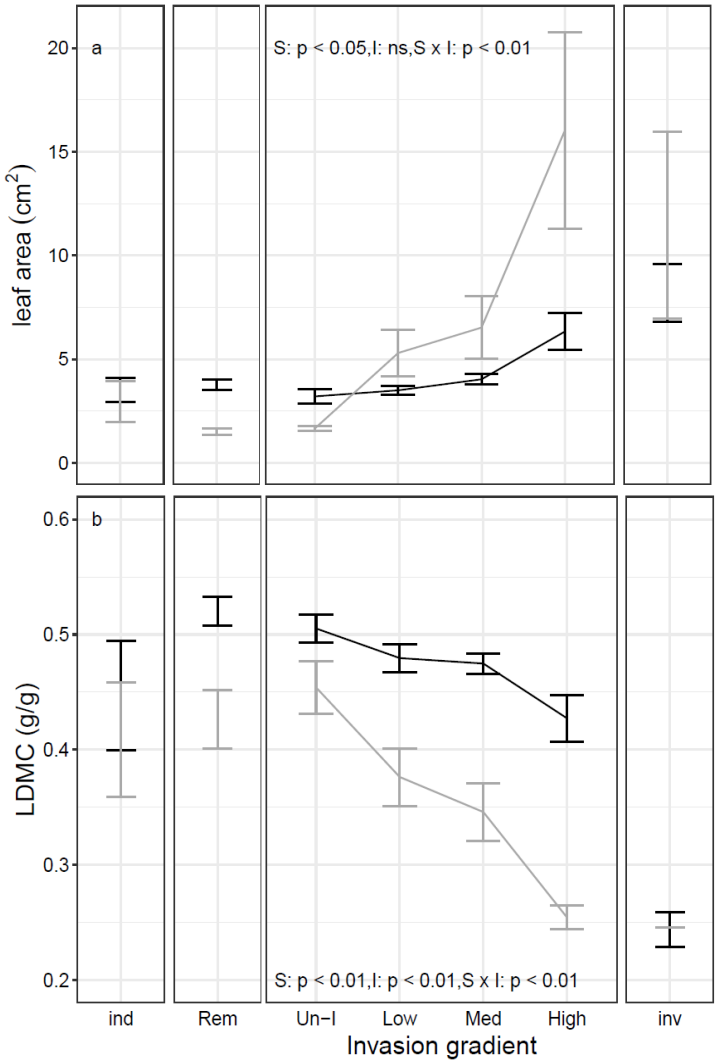

Figure 1: Trait means across invasion gradient in two savannas (black- BLS, gray- FLS). Community weighted means (± SE) of traits a) leaf area and b) leaf dry matter content (LDMC) across invasion gradient. Mean (± SE) of indicator species and invasive species in each savanna. Rem - Remnant plots which represents old growth savannas; Low, Med and High were plots with low (~30 %), medium (~50%) and high (>80%) cover of invasive species. ind are indicator species of old growth savanna and inv are invasive species of each savanna.

In the following section, I summarize some of the drawbacks of the current study and emerging questions. In the second chapter of the thesis I used Herbaria and Floras to study range size and spread rate two of the crucial dimensions associated with invasion of species. Although, data from herbaria and Flora are essential to understand spatial distribution of species over time, there are certain issues with relying solely on them to understand range size of species. Due lags associated in collection efforts made by herbaria these data source need not always align with the current range sizes of species which were historically widespread but since has reduced its range. Additionally, recently introduced species with shorter lag times, will not be picked as problematic if I rely only on herbaria data (Antunes and Schamp 2017). I have therefore also used information from experts regarding the current spatial distribution of species. However, these results can also be often biased. Future studies must therefore use field work or GIS based approach to map the spatial distribution of these invasive species in NWGK. Occurrence data from herbaria can supplement these studies to study more nuanced patterns of spatial change over time.

In this thesis, I compared functional trait with invasion success of species. I looked at different dimensions of success but it's important to recognize that all the species under consideration are already invasive in this region. To get a more clear understanding of how traits contribute to success one must compare traits of invasive species with naturalized and casual aliens introduced around same time. Identifying traits related to this transition is important for effective risk assessment and management. Previous study from the subcontinent has shown that LMA is associated with naturalization success but this study was not comprehensive and had analyzed only three of traits (Banerjee et al. 2021). Furthermore, it is important to understand if the traits

responsible for success of non-native species in a region also explain the success of the native species in this region. Future studies should identify widespread, locally abundant problematic native species and compare their trait with invasive species (Hejda et al. 2019; 2021).

In final two chapters I show that a few indicator species are preferentially lost upon invasion, whereas certain native species which are frequently found in the invaded communities. Interestingly, invaders have more similar traits with the co-occurring natives than the indicator natives which are never found in invaded plots. One can therefore speculate that invaders preferentially replace species having dissimilar trait composition. However, our study is an observational field study, and plots could have differed along factors which could not be controlled for such as disturbance intensity and microhabitat conditions (Stricker et al. 2015) . In absence of such controls, it's difficult to conclude with certainty if the trait differences are an effect of invasion impact or is influenced by these other factors. Therefore, I suggest that future study should conduct greenhouse and manipulative field experiments to identify if and which traits are related with competitive exclusion by invader in these savannas.

Conclusion

Invasive alien species are the leading cause of biodiversity and socio-economic loss in the world (Vilà et al. 2011). Last couple of decades has seen an exponential growth in number of non-native species around the globe. Scientists and policy makers around the globe have recognized the pressing need to identify, prioritize and control invasive species before more damage is done (Bacher et al. 2024). This thesis fills a major knowledge gap by identifying, characterizing and prioritizing invasive plants from the Northern Western Ghats and Konkan regions. Despite the

growing concerns related to impact of invasion, this biodiversity hotspot is not well studied. Threatened ecosystems in and around the Ghats must be prioritized for conservation. While this thesis provides information on areas and species that needs to be prioritized, a lot needs to be done in order to control the impact of the species in region. This thesis shows that trait based approach is a promising field to understand plant invasion and future studies must explore this approach to screen, manage and control invasive plants.

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