MODELLING PLANT INVASIONS IN TROPICAL FORESTS OF INDIA

THESIS
SUBMITTED TO THE
FOREST RESEARCH INSTITUTE DEEMED TO BE UNIVERSITY
DEHRADUN, UTTARAKHAND

FOR
THE AWARD OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN FORESTRY
(FOREST GEO-INFORMATICS)

BY
NINAD AVINASH MUNGI

WILDLIFE INSTITUTE OF INDIA
DEHRADUN, UTTARAKHAND

2019

DECLARATION

I hereby declare that the thesis titled "**Modelling plant invasions in tropical forests of India**" submitted by me (Regd. # 13PHD282) to Forest Research Institute (Deemed) University, Dehradun, for the award of the degree of Doctor of Philosophy in Forestry (Forest Geo-informatics), is a record of original research work carried out by me under the supervision of Prof. Qamar Qureshi and co-supervision of Dr. Y.V. Jhala, both Scientist-G at the Wildlife Institute of India, Dehradun. It has not formed the basis for the award of any other degree or diploma. I also declare that the thesis embodies my own work, observation and analysis; and in that respects the investigation appears to advance knowledge in the subject.

Ninad Avinash Mungi

Place: Dehradun
Date: 26th August, 2019

Countersigned:

Jhala

Qamar Qureshi, M.Phil
Supervisor

Y.V. Jhala, Ph.D.
Co-Supervisor

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that the thesis titled "**Modelling plant invasions in tropical forests of India**" submitted by Mr. Ninad Avinash Mungi, (Regd. # 13PHD282) to Forest Research Institute (Deemed to be) University, Dehradun, for the award of the degree of Doctor of Philosophy in Forestry (Forest Geoinformatics), is a record of bonafide research work carried out by him under my supervision. No part of this thesis has been submitted for any other degree and it fulfils all the requirements laid down in the ordinance of the Forest Research Institute (Deemed to be) University, Dehradun for this purpose.

It is also certified that the thesis has been duly evaluated for plagiarism through URKUND, and reported to be within the permissible limits.

Jhala.

Prof. Qamar Qureshi
Supervisor
Scientist – G, Wildlife Institute of India

Dr. Y.V. Jhala
Co-Supervisor
Scientist – G, Wildlife Institute of India

Place: Dehradun
Date: 26th August, 2019

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APPENDIX - 7

FOREST RESEARCH INSTITUTE DEEMED to be UNIVERSITY
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This is to certify that **Mr. Ninad Avinash Mungi** enrolment no. **13PHD282** carried out research work under **Prof. Qamar Qureshi and Dr. Y.V. Jhala** of the **Wildlife Institute of India, Dehradun**. The topic of the research registered with FRI Deemed to be University was '**Modelling plant invasions in tropical forests of India**'. The scholar presented his work in the pre-thesis submission seminar held on **16th August 2019** and the RAC found the work to be satisfactory and approves the work to be presented in the form of thesis for evaluation by examiners for the "Award of Ph.D. Degree" by FRI Deemed to be University.

Prof. Qamar Qureshi
Supervisor, Scientist – G
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To

Mr. Ninad Avinash Mungi,
C/o Prof. Qamar Qureshi, Scientist-G,
Landscape Level Planning and Management Department,
Wildlife Institute of India,
P.B. No.18, Chandrabani, Dehradun – 248 001,

Sub:- Registration for Doctor of Philosophy Degree in Forestry.

Dear Sir/Madam,

I would like to inform you that the following decisions have been taken for your enrolment as Research Scholar for the Degree of Doctor of Philosophy in Forestry in this Institute:-

1. You have been registered for Doctor of Philosophy w.e.f. **01.03.2014 to 28.02.2018** as Ph.D Research Scholar.
2. Your Enrolment number is: - 13PHD282
   (For all further correspondence please quote your enrolment number.)
3. Name of Research Centre: - **Wildlife Institute of India, Dehradun**
4. The Topic of research approved by the FRI University: **"Modelling plant invasions in tropical forests of India."**
5. Name of Discipline: - **Forest Geo-informatics**
   (As per clause 3.3 of the Ph.D. Ordinance)
6. (i) Name of Supervisor :- - **Sh. Qamar Qureshi**
   (ii) Name of Co-Supervisor:- - **Dr. Y.V. Jhala**
7. (a) You are advised to **deposit the next installment of Laboratory fee Rs. 5,000/- payable at FRIDU/Research Centre concerned through bank draft in the month of March, 2015**
   (b) Library fee of Rs. 2,000/- per year payable at FRIU/Research Centre concerned in the month of March for each year of registration till submission of thesis.
   (c) **Annual fee of Rs. 10,000/- payable every year in the month of March** during the period of Registration at FRI University till the submission of thesis.
   (d) The above mentioned fee should be deposited during the due month i.e. March every year failing which a late fee of Rs.500/- (Bank Draft) will also have to be deposited in this office.
   (e) You are also required to deposit the thesis fee Rs. 15,000/- and viva-voce exam fee Rs. 2,000/- at the time of submitting the thesis and viva voce exam respectively to the University.
   (f) In case of extension of term of registration, the extension fee will also be charged. (Ist time Extension fee Rs. 25,000/- and for IInd time Extension fee Rs. 40,000/-).
8. The research scholar is required to submit the six monthly progress report till the work is presented in the pre-thesis submission seminar and is approved by the committee for submission of thesis.
   The initial 4 progress reports may come through Chairman and Member Secretary R.A.C. The rest can come through Head of Division and Supervisor concerned. **The RAC shall consider the progress reports and forward the same with recommendations and comments, if any, to the Registrar, otherwise the progress report will not be counted.**

P.T.O.

i. Two consecutive six monthly progress reports are not submitted at all or are not satisfactory.
ii. The attendance of Research Scholar is less than 75% in any term.
iii. The scholar violates the clause 4.3 of the Ph.D ordiance regarding compulsion of 2 years Study leave for pursuing Ph.D in Case of in service candidates (except the employees of ICFRE and Research Center of FRI (Deemed) University).

10. No internal Ph.D. Scholar shall accept during the period of research any paid assignment apart from Research Fellowships, Research Assistantship etc. unless in the opinion of the RAC such an assignment will not interfere with his/her research work.

11. A Ph.D. Scholar shall not be permitted to take any other degree course, but may be permitted by the RAC to take part-time Diploma or Certificate course(s) not affecting the scholars research work adversely.

12. **A Research Scholar is required to pursue research in the Institute/Research Centre under the Supervisor on the approved subject for not less than twenty-four months commencing from the date of his/her registration.**

13. **The Research Scholar may not later than three months from the date of issue of registration letter, modify the scheme of the research work or nature or scope of the subject, on the recommendation of the Supervisor and RAC, with the approval of Director.**

14. As per clause 6.14 of the Ph.D. Ordinance, the Ph.D. scholars shall publish atleast one research paper in a peer reviewed journal before the submission of the thesis to the University for evaluation, and produce evidence for the same in the form of acceptance letter or the reprint. The acceptance letter or the reprint should be attached along with the thesis in the annexure.

15. **The research scholar should normally submit the thesis within 4 calendar years from the date of registration. Further extension of the term on yearly basis is possible only on specific recommendation of R.A.C., if approved by the R.D.C. However no extension is possible beyond 6 years of registration. The recommendation of Research Advisory Committee for extension of term of registration of the scholar should reach this office before expiry of term of registration.**

16. Further the performance of the Research Scholar shall be evaluated at the end by the R.A.C. concerned in the pre-thesis submission seminar and R.A.C. shall send the minutes to Registrar, FRI University with full comments.

17. **Please ensure that the clause 7 of the Ph.D. Ordinance is fully complied with before submission of the thesis to University.**

18. **Please note that your Registration as Research Scholar is to be governed as per rules, regulation and ordinances of FRI University, with applicable amendments made by the University from time to time. For all further correspondence, please quote your enrolment number.**

(Dr. A.K. Tripathi)
Registrar
FRI (Deemed) University

Encl: 1. **Fee receipt No.747 dated 25.08.2014 for Rs. 26,500/-**
2. **Format of progress report**

Copy to:

1. Sh. Qamar Qureshi, (Supervisor of the Scholar) Scientist-G. Landscape Level Planning and Management Department, Wildlife Institute of India, P.B. No.18, Chandrabani, Dehradun – 248 001, for information and necessary action.
2. Dr. Y.V. Jhala, (Co-Supervisor of the Scholar) Scientist-G, Department of Animal Ecology and Conservation Biology, Wildlife Institute of India, P.B. No.18, Chandrabani, Dehradun – 248 001, for information and necessary action.
3. Dr. K. Sankar, (Nodal Officer) Wildlife Institute of India, P.B. No.18, Chandrabani, Dehradun – 248 001, for information and necessary action.

(Dr. A.K. Tripathi)
Registrar
FRI (Deemed) University

Acknowledgment

"Conservation is like a beautiful painting we wish to paint, each color and every stroke is to atone our collective reality" - *Qamar Qureshi, a winter evening in 2012*

QQ threw this statement as an answer to 'how to conserve the system, if it crosses the tipping point?' He was then teaching me Krebs and quantitative ecology for more than four months, no doubt I reflected on his ideas and was thrilled by his scientific challenges. That evening I cancelled my PhD application elsewhere and decided to pursue his supervision. Foremost in acknowledgements, I thank QQ for inculcating in me, a courage of questioning, patience of enquiring and curiosity of exploring. I thank him for being a person with whom I required no filters in personal relations, and no worries in scientific endeavors; for he was always there to make me learn through my experience, with a gentle smile and "*Aur bata...*". While this relation with QQ was a luck factor, my relationship with my PhD co-supervisor Dr. Y.V. Jhala was more of an evolution. Let me admit that initially I was only under an awe of his reverence in the scientific community, like most of his fans. But later, when he sat with me for days to frame every statement in my first scientific paper, I was stunned at his uncompromised love for accuracy and precision. I became his fan, and that too like everyone else - on field. More than anything, he is my personal role model, for his contagious youthful personality! I think I've been lucky to get the best combination of guidance that I've ever seen. This thesis grew out of the discussions between QQ and Dr. Jhala, and so did my life. While I basked in the light of the 'largest data', this duo kept me grounded to the fundamentals of science. Personally, they improved me by challenging by belief system, as well as providing a liberal workspace. I've hardly discovered such a combination of respect and freedom in any person.

My thesis is the first, to come out of the world's largest wildlife survey - All India Tiger Monitoring Program. A decade back, many scholars debated (vehemently) that if tiger could be used as a flagship species to monitor the changing forests. My thesis exclaims Yes! It was due to the pioneers of tiger project who could forge science in the name of the tiger, that I relish the rich fruits; and many would in future. I thank the National Tiger Conservation Authority (NTCA) for putting together the plan, system and resources for undertaking this sampling. I thank Dr. Rajesh Gopal for supporting and inspiring my work. His comments and observations on invasive plant management, during our meetings in Bar-Nava Para provided me insights on the necessity of evidence-based conservation. I thank the state Forest Departments who coordinated the sampling from more than 700 divisions, where the Division officers, Range officers and Beat guards have been making this survey a success. I thank the research team from each cycle of the sampling, who through their arduous efforts, have put together the data and bequeathed it for posterity. I joined the Wildlife Institute of India (WII) as a volunteer in the sampling cycle of 2011, and I know how each of the research personnel wished best for this program, it is this faith that inspires me to continue the quest of science-based conservation in this country.

The WII has been a substantial part of my youth, where I could take freedom to accomplish my scientific endeavors. Through all these days the administration of the institute has been helping me in the best possible way to conduct my research. I express my gratitude to Dr. V.B. Mathur who has been supporting my work on invasive plants by showcasing it in the India's Fifth Report to the Convention of Biodiversity, and for organizing the workshop on 'invasive species management' - results of which are exclusively written in Chapter two. I'm personally indebted by his encouragement for me to apply for the IPBES fellowship, which made my research reach a global platform. I thank Dr. G.S. Rawat for teaching me biology of invasive plants. His ideas on how tropical plants are invading in Himalaya helped me write a paper on relating the climate change and invasive plants in Bhagirathi valley, results of which is part of the chapter seven in this thesis. I thank Dr B.C. Sinha for availing the research facilities, professional requirements, helping me on personal fronts many times, and providing the coziest place to stay - Old Hostel. One person who has been as concerned as my parents about my PhD completion was Dr. V.P. Uniyal. He has been helpful and supportive to get my official updates done and make my PhD in time. I thank the research advisory committee members who provided their constructive suggestions to improve my thesis and finalize it. I thank Dr. Gautam Talukdar, Dr. Navendu Page, Dr. S.P. Goyal, Dr Vishnupriya Kolipakam and Dr. Amit Kumar for it. I remember how Dr. K. Sankar helped me personally during my PhD registration, due to which I could enroll in this program; I am indebted by his favors. I thank the PhD coursework coordinators Dr. Gopi G.V. and Dr. S.K. Gupta for making the coursework interesting by encouraging scientific review writing, which is now chapter one of this thesis. I thank Dr. K Ramesh for his help during my internship in Canada. I extend my gratitude to all the faculties and scientists in the WII, who have always helped me on a professional, academic and personal front. I thank Shri. P.K. Agarwal for supporting me and my research through all capacities.

I thank the Forest Research Institute (Deemed) University, Dehradun, for facilitating my PhD research. Madam Bharti from the PhD department has been a great help and support throughout my PhD. I thank the Registrar, for the support and help.

Spending the most crucial and productive years of life for research in conservation science and ecology, is a risk for many financially unsecured young scholars. I very well understand the limitations of doing science without earnings. But it was benevolent funding agencies like the Queen Elizabeth Scholarship program that recognized the necessity for knowledge exchange between the developed and developing countries, and through which I could be a QEScholar and avail an internship at the University of British Columbia (UBC). During my internship at UBC, Dr. Nicholas Coops made me learn techniques in remote sensing and climate change science, which helped me explicitly in working on the chapter seven of my thesis. He and his research team (IRSS) provided one of the finest memories of experiencing the temperate rain forests on Vancouver Island; Thank you IRSS! When I remember my life in Canada, it always reflects favor and friendship with Jorma and Laura. They provided me with everything from my kitchen to a hike on a glacier. Other funding agencies like the Science and Engineering Research Board (SERB - DST), National Trust for Nature Conservation Nepal, Society for Conservation Biology's Asia Chapter, International Congress for Conservation Biology, FAO Asia Pacific, and Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services helped me to showcase my research to the global audience and provide me an opportunity to network with peers and learn from them. I am thankful to Madhya Pradesh state forest department (SFRI), Uttarakhand state forest department, Bihar state forest department and Rajasthan state forest department to provide me data on the management of invasive plants and fund me to visit invasive plant management sites in different protection zones of the forest department.

I have been part of one of the busiest research teams in the WII - the Tiger team. Foremost, it would have never been possible for me to complete my PhD, had I not had cooperative colleagues. I thank my MSTrIPES team - Ashish, Anup, Ashok, Ahana, Akshay, Debranjan, Krishna and Kainat for always helping me in the project accomplishment and granting me windows of escape to complete my thesis. I thank my colleagues who were for a part of time on the MSTrIPES - Gaurang, Madhura, Rahul Rana, Rohan, Abbas, Saugata, Srinivas and Papori. I thank the Tiger people - Kausik da, Ujjwal bhaiyya, Swati ma'am, Neha, Shikha, Ayan, Manjari, Sudip, Jayant, Shravana and Mutthu jee for their inputs in improving my knowledge and skills. I joined WII as an alien species, with no background in ecology, it was due to these colleagues that I could naturalize and learn much.

I was fortunate to get friends, who taught me the nuances in science; for this I thank Sutirtha Dutta, Merwyn Fernandes, Vishnupriya Kolipakam, Malvika Oniyal, and Bipin CM. And then there were teacherly friends who accompanied me on the journey of learning; thank you Sabuj Bhattacharyya and Monica Kaushik. These two have been on secret service of making me successful, as well as a drama queen. I thank Amrita Laha for adding to my understanding of social sciences, making me appreciate the ounces of happiness in life and giving the ultimate *shurshuri*. I thank Yogesh S for changing my thought process completely and being an era of enlightenment in my life.

Neeraj and Ankita Bhatta - bleh...;)

Dehradun life had a substantial contribution to make my PhD years stress free. It would not have been so, had I not got few amazing happening friends. I came to Dehradun with my MSc batch mates from Pune university, Pranita and Sagar. With Pranita, I explored the place and created stories together. Stories that will comfort my memory lane in the grey academic years. With Pariwa, I remember walking on the trail with evening chai and watching the emerald of spot-billed ducks on one side and golden lights on the *Saccharum* inflorescence on the other, that eased my lab stress. On weekends with Priyamvada on the Himalayan foothills, her bike and our stories would never stop; my fav labmate! Another weekend brand was outing with Swati ma'am and Ridhima, what a lovely time and memories has this duo gifted me, thanks! More than my own eyes, I've seen Dehradun changing from Swati ma'am's eyes. Be it eating litchis under the *Ziziphus* tree in the veranda with Devanshi, or feasting on momos at Thapajee's place with Preeti, Madhura and Shivam, Dehradun has offered the best memories in each form. Subhashree not only allowed me to invade her place, but she was a place, where I could unfold and rest! And how then can I forget late-night parties in the 'red' room with strings of guitar and the perfect cocktail of pahadi and bengali voices; things I miss the most. Thanks to my PhD life!

Now, after spending splendid nine years in Dehradun, and seeing it change, I often feel that I have an extended family who connect me to the city and its life. Foremost, I thank Dr. Nita Shah for motivating me to complete the thesis on time and work on both - actions and publications. My early internship with her on vulture distribution, helped me learn the nuances in policy execution and need of proactive participation using scientific evidence. Her enthusiasm for field biology on the one hand and on the other a motherly care of feeding us amazingly delicious food, had made many of my memories feel homely in this place. Food and fun remind me of a recent interaction with Rajeshwari Madam, talking with whom have been refreshing and amazing. Another home that I discovered in Dehradun is of Swati ma'am. The way auntyji would feed us all with delicious food followed by an amazing chai has been simply lovely. Home of Pariwa, is similar feeling; just a difference that I call her mother with a pet name, and I think she doesn't hate it beyond a point. They ensure my participation in most of the family gatherings and it warms (or cools) my heart. A couple that made their routine feel like home to me was Ujjwal bhaiyya and Neha, who exemplified the Indian way of working together as a family, and making professional space easy. These family extensions made me stronger to face, at times, obvious depressing phases in the PhD life.

Thanks to Hussain for taking me on wonderful journeys and making me see Himalaya the way he saw. I thank Mr. (sone to be Dr.) Pankaj Raina for building my aspirations in the last months of PhD, when they are really required. His appreciation of my work, by availing me an opportunity for working in the Trans-Himalaya, is a receipt of my successful learning; thanks Pankaj bhai! It was with Anchal, Dimpi and Niaz that I saw this new world of trans-Himalaya, and I am thankful for that. Next comes my obvious weekend partner, with whom I've been so engaged on any holiday, Mr. Prabir De. Though our interaction was a product of MSTrIPES, he has helped me generously by providing 'hints' to get spatial data from various administrative sources. His staff at the SCIENCE, particularly Arun, has been a great help.

My Old Hostel friends; by now they are a significant part of my life. I express my gratitude to each of them for the endeavors in research, life, late-night philosophies, early morning birdings, bonfires, parties and digesting mess food. Thanks Ridhima, Parabita, Nilofer, Ankita Sinha, Shagun, Pallavi, Akanksha (CL), Vaijayanti, Upma, Shruti, Samhita, Sazia, Divya, Bibek, Bopanna, Kamlesh, Ganjendra, Ishwari, Suresh, Sajal, Nilanjan, Rahul, Keshab, Nishant, Stotra, Indranil, Srinivas, Azaz, Shashank, Ravi, and many others. I've seen three MSc batches in WII, and it so happened that I collected few amazing friends from them. I don't want to name a few, for I fear to forget others, but I appreciate all the help from the students of XIV, XV and XVI MSc batches. I thank Arjun, Tushna, Nakul, Ankush, Rutu, Parul and tiger project researchers for so many dinners and chats, though you all came to my life way recently, I'll always cherish our common memories. Thank you Harshini for being there whenever I wanted to rant, planning so many papers together. I'll always cherish our field memories of Kanha with Dhananjay and Stotra. One of the homeliest feeling that I received in WII after Madhura, was that from Ashwin and Swaroop. This rare unshaken pair in the history of WII, has been simple lovely. Our discussions and confident opinions on many things that neither of us ever read, connected us more than anything; a trait common to our native place ;)

People from the academic and administrative sections of the WII has been extremely helpful in making my life easier; I thank them all. Gyanesh jee have been extremely helpful since I've started my PhD registration. Uniyal jee have been helping me to settle all the documents and yearly reports. Baluni jee have been another amazing support, who were much informed about our financial crises and tried to help us best by providing our fellowships and field allowances on time. People from the IT and GIS section have been helpful in many ways, I thank Rajesh Thapa sir, Manoj Agarwal sir, Panna Lal sir, V Sukumar sir, Alka Agarwal madam, Virendra Sharma sir, Ankit, Jeet, and all other members of this section. I thank Zeeshan, Anupama, Aadarsh and Nupur for being amazing labmates. I thank Babita madam, Shweta, Ishi and Vinay jee for keeping a track of my supervisors and secretly providing it to me. I thank Shambhu bhaiyya and Devendar bhaiyya for always being there, whatever I need - plain sheets, printer, files or chai, they were always there to provide it. Sai jee was very supportive in maintaining my GIS lab, where I have spent the most substantial part of the last nine years. I thank the old hostel staff Vinod, Aswal jee, Pawan, Bhim bhaiyya, Rakesh bhaiyya and all mess staff for amazing service and help.

While I spent all these years in Dehradun, my friends in Pune reminded me to return. But while doing so, they stood with me in my decisions and with my family in my absence. I thank Omkar, Suhas jee, Yuvraj, Govande family and Joshi family for being an amazing support. I thank my extended families in Pune- Belsare, Kulkarni, Joshi, Waikar and Kulkarni, for all their support and encouragement. I thank my cousins Sayli, Swarali, Rohit, Ved, Kedar, Kshitija and Neha, and their partners, for always being there and appreciating my research.

Now, when I think of what I thought of my post-PhD life strategy, it was often research but staying with my complete family. Since I've registered for my PhD, I lost both of my grandfathers, who till the last moment kept asking me when I would be a Dr. I remember how despite seeing me for only once a year, these Alzheimer old eyes remembered me. They have inspired me to put my best effort in making this PhD successful and useful for others. My grandmothers, who are now more wrinkled, wait for the day when I would finally be PhD. It is for these two young ladies; I have completed my PhD on time. Talking of my parents, Aai and Baba, words fall short to express my gratitude for their role in my research. The confidence that they have shown in me and the ambience of freedom that they have provided has made my life choices so easy. Without expecting any of my time, any kind of participation or involvement, this duo has been busy in making me successful and stronger every day. Aai could not believe when I told how her interest in plants during the time when we stayed in a dry Savanna of central Maharashtra, developed my personal relations with seasons and plants. Her passion for clean work and micromanagement, and her love for making our lives comfortable has taught me a great deal in research ethics. Baba has been a person, like whom, I wish to love someone someday - selflessly. It so happened that whenever I was down or stressed by work, I somehow got his phone call and then we talked about everything, from my issues to the national issues. When I often romanticize about my research and the forest, my parents remind me of a *Ficus* tree in the middle of a rugged savanna, along a small water stream, with boulders to sit upon. A scene that I often remember, whenever I imagine my childhood, my home, my heart; and a scene I wish to preserve amidst the chaos of emotional and global homogenization. I dedicate my PhD to my parents!

Then comes an apology for the person who bears the burden of my hopes and dreams, my sister Pooja. I remember her when I left home nine years ago, our lives have changed so much. I just wish I could have spent all this time with her, I wish I was there in all the fun times when she was happy for no reason, and when I was down for no reason. She builds my aspirations and motivates me for doing the best of my efforts. I remember her efforts to recognize small steps in my professional life and make me feel special about it. The only companion with whom I dare to grow and succeed in my personal life is her. She's my home, where I shall return.

At end, I thank my life partner Rajat Rastogi, who has taught me ecology, compassion, love and much more. Support from this invasion ecologist enriched my thoughts on the subject. Besides learning how to love, I learned my field techniques from him. Personnel life often sheds due to academic stress, but he ensured that I got a healthy one. He ensured I build hopes and dreams bigger than academia for being a person who can deserve love! Thanks boo. Thanks for giving me another home in Mawana, who support our endeavors. And thanks for being my life.

At the end, I feel fortunate to have been in a culture, where the realism is contested as a function of endless enquiries, each enquiry - however perfect and complete - is only a possibility. While I present results from the largest wildlife monitoring, I understand that within the ambit of knowledge these results only bring possibilities. I hope it brings a possibility, through which the reader and the user of this study could be benefited. This utility will be my reward, which I would like to dedicate to everyone acknowledged here.

Athato Brahma Jijnasa...

Ninad Avinash Mungi

Dehradun
भाद्रपद 2, शक संवत् 1941
24th August 2019

Executive Summary

1. Human modifications are simplifying global ecosystems, and one agent catalysing this process is biological invasion. Species transferred by human means to areas beyond their evolutionary range, where they impact the native ecosystem and its services, are known as invasive species. Invasive species have affected native ecosystem functioning to an extent where native species went locally extinct, or where the native economy and human health has been adversely affected. While invasive species are spreading at an alarming rate, our knowledge on their large-scale status remains disjunct, disparate, and often outdated. The resultant loss in global ecosystem services is believed to be catastrophic for the global human-welfare; with developing societies being the most vulnerable. One such megadiverse developing country is India.

2. Unlike other tropical developing countries, where forested areas are reducing to the increased developmental activities, forest area in India was reported to increase at an overwhelming high rate over the last decade (1120 km^2/year). Few studies flag that this increase could be misleading due to inclusion of non-native plantations and exclusion of quality in defining the 'forest'. Amidst the controversy of increased forest cover, marked lacuna in national-level initiatives for mapping invasive plants' spread is impeding timely management actions. Present thesis investigates the spread of 11 High Concern invasive plants in India (*Ageratina adenophora, Ageratum conyzoides, Chromolaena odorata, Hyptis suaveolens, Lantana camara, Mikania micrantha, Mimosa diplotricha, Parthenium hysterophorus, Prosopis juliflora, Senna tora* and *Xanthium strumarium*). Within the ambit of this thesis, I address three questions 1) what is the spatio-temporal rate of plant invasions in the tropical forests of India? 2) What facilitates or resists invasion in different vegetation types? And 3) Given the global change scenarios, where will invasive plants spread in the future?

3. The government of India has used All India Tiger Monitoring Project (AITMP) as an umbrella project that ensures of using tiger's charisma to garner resources and public support for securing natural systems along with their functions. The AITMP monitoring protocol for assessing habitat status is used to systematically sample forests in 19 Indian states for collecting information on invasive plants in a scale of 5 X 5 km grids. Within each forested grid cell, 1 or 2 transects of 2 km length were walked. On these transects, at every 400 m a circular plot of 30 m diameter was sampled. Within each plot, all plants (native and invasive) were recorded to their abundance. In the same plot, sign of human disturbances were recorded for indexing wood extraction and grazing pressure. Sampling was repeated four times since its initiation (2006), thereby sampling an area of 169,002 km^2 in 2006; 203,810 km^2 in 2010; 278,675 km^2 in 2014; and 162,441 km^2 in 2018; within which an area of 86,700 km^2 was consistently sampled across the years. This is the largest known systematic sampling for invasive plants globally.

4. To understand if these invasive plants had potential niche in India, which was realized following the species introductions, I assessed the climatic and biotic niche of these plants based on their native range and compared it with India. This was done using niche models for projecting species' native niche to model its potential niche in India and then comparing it with species' observed niche in India. Niche models are however vulnerable to the taxonomic unit used for comparison, the area selected to compare, parameters used to define niche and limited data. I address these limitations by including various taxonomic ranks, ecological hypothesis based niche axis (climate, resources, competition from the forest cover, and anthropogenic modifications), modelling environmentally analogous areas within the native and invasive range by using the world's largest systematic database on invasive plants. This also helped me to test MacArthur's hypothesis, which suggests that species might utilize their congenerics' niche in invasive range, which was prevented due to congeneric competition in its native range. This was done by independently projecting the invasive species niche and its genus' niche from the native

range to India; and comparing the species niche stability, expansion and unfilling using its observed niche. Subsequently. we compared the niche changes on climatic axes and biotic axes.

Results suggested that when only the taxonomic rank of species was considered while comparing difference in projected and observed niche for invasive plants, 10 out of 11 species showed a significant expansion (P-value < 0.1) of their climatic niche while all species showed expansion in biotic niche. But when the species niche in India was compared with the projected genus niche, only a few significant expansions were observed. A significant increased expansion towards higher temperature, lower soil fertility, denser canopies and higher evapotranspiration rate was observed for *Ageratina adenophora, Ageratum conyzoides, Lantana camara* and *Chromolaena odorata*; while a significant increase to higher rain in the driest season, higher soil fertility and lower evapotranspiration was observed for *Prosopis juliflora, Xanthium strumarium, Hyptis suaveolens*. Invasive plants extended their optimum phenotypic functioning to exploit the environment colonized by their congeneric species in their native region. While the expansion of species to utilize their genus niche in invasive range indicates their niche conservatism, few species significantly expanded their niche beyond the genus niche. This trait shift indicates species' phenotypic plasticity, which, if responsible for its higher fitness, could be considered adaptive. In the light of an extended phenotype in most of the tropical organisms, I interpret this phenomenon as 'niche plasticity'.

5. While most of the global changes have reduced native species, invasive species, on the contrary, have been facilitated by them. Hence, there's a recent surge in understanding how the changing earth system is driving invasive species distribution. For this I investigated the multi-scale drivers of invasive plants in tropical forests of India. These drivers were classified as climate (maximum and minimum temperature, annual precipitation and precipitation of the driest quarter), resources (water availability), forest cover (canopy cover and deciduousness of the

forest), forest fragmentation (fire, forest loss and index of forest browning) and anthropogenic pressure (night-time lights and distance from human infrastructure). I used seven spatial scales (250 m, 500 m, 1 km, 2 km, 5 km, 10 km and 20 km) to model the effect of these drivers. Maximum Entropy (MaxEnt) models were used, as MaxEnt can incorporate non-linear relations and is known to perform well for modelling species distribution. However, each covariate has a natural operational scale (calculated by Moran's I), below which it is spatially auto-correlated. For each species, we generated an inter-scale ensemble model by weighing the distribution models at each scale by the contribution of each driver and the spatial independence index. Inter-scale ensemble model has been developed for the first.

Model performance decreased with increased grain size (slope = -7.2, $R^2 = 0.91$, $P < 0.05$), and the optimal scale at which the modelling accuracy was ≥75% for all species was 1 km. The average contribution of drivers differed with scale; it increased for climatic drivers (slope = 15.1, $R^2 = 0.98$, $p < 0.001$), decreased for canopy cover (slope = -5, $R^2 = 0.99$, $p < 0.001$), water (slope = -10, $R^2 = 0.97$, $p < 0.01$), and disturbance drivers (slope = -8.3, $R^2 = 0.97$, $p < 0.001$). The distribution estimates across the scales for all species increased with scale; but the average accuracy of modelling presence and absence (derived using True Skill Statistics) was highest (≥ 75±8%) for the interscale ensemble model, as compared to individual scale models. Also, the response of same species for the same driver (particularly with resources and disturbance drivers) was different at different scales; and only inter-scale ensemble preserved these ecologically meaningful responses. This suggests that invasive species take advantage of small scale disturbances that likely initially facilitate them, and then spread in the favourable climate at larger scale; thus, displaying plasticity for multi-scale nested drivers of the landscape. However, this further requires primary data for multiple years to validate the drivers that either facilitate or resist invasions.

6. To evaluate the rate at which invasive plants are spreading in the tropical forests of India, and confirm the key environmental drivers that are facilitating them, we used the occurrence of invasive plants from a common sampling frame across 2006, 2010 and 2014 in a dynamic occupancy modelling framework. This framework not only helped us identify site covariates that explains the probability of occupancy (ψ), probability of invasion (γ) and probability of extinction (ε); but also corrected for the probability of species being present in the grid and not detected in the plot (P). As P might vary across the years, it was kept as a function of sampling year. ψ, γ and ε were modelled as a response to nearness to previously invaded areas, water deficit, forest edge density, timber extraction, livestock grazing, urban spread, climatic drivers and greening and browning of forests. In order to include the difference in species response across the biogeographic realms, we independently analysed the dynamic occupancy for all species in the dry forests and moist forests. Results suggest that across all the species in both forest types, γ was best explained by the nearness of the site to other invaded areas in previous sampling cycles; ε was best explained by null model while ψ differed for species and forest types. When the average response of the same species to the same driver was compared in dry and moist forest, we found that occupancy of invasive plant was facilitated by urbanization index, forest edge density, timber extraction, warmer temperature of winters. However, the majority of species that invade in both forest types (dry and moist) had an altered response to other drivers. While higher rainfall and greening of the vegetation positively explained their occupancy in the dry forests, it had negative relation in moist forests. Water deficit, livestock grazing and fire frequency positively influenced invasive plants in moist forests, and negatively in dry forests.

The average net gain in invasion area per year, after correcting for detection and site covariates across forest types for different invasive plants was: 440 (±62) km^2 for *Ageratina adenophora,* 586 (±106) km^2 for *Ageratum conyzoides,* 735 (±214) km^2 for *Chromolaena odorata,* 242 (±78) km^2 for *Hyptis suaveolens,* 890 (±369) km^2 for *Lantana camara,* 954 (±278) km^2 for *Mikania* *micrantha,* 188 (±46) km^2 for *Mimosa diplotricha,* 153 (±102) km^2 for *Parthenium hysterophorus,* 761 (±337) km^2 for *Prosopis juliflora,* 310 (±152) km^2 for *Senna tora* and 220 (±119) km^2 *Xanthium strumarium.* Results suggested that invasive plants were spreading around existing invaded areas. However, the occupancy was positively related with the degraded drier areas in moist forests and productive water rich areas in dry forests. In India, moist forest areas are being fragmented by different developmental activities and global changes, while dry forests are being irrigated and greened by plantations and agriculture. Results suggested that these are favourable conditions for the alarming spread of invasive plants.

7. Invasive species, climate change and anthropogenic disturbances are interactive and pervasive challenge to the world's biodiversity. These challenges are more severe in the tropics, and facilitate the spread of invasive plants. Hence, it is essential to understand how our democratic choices in land use change, agriculture, energy and forest management can influence the future of invasions in India. For modelling the future projections of invasive plant distribution, we built two alternate pathways for every 10 years (year 2020, 2030, 2040 and 2050) that would lead to either 'business-as-usual' scenario or 'sustainable future'. For 'business-as-usual' scenario, I retained the trends in urbanization, agricultural productivity, irrigations, drying water channel, mining, intensity of invasive species management and climatic pathways (RCP 8.5) as observed for the last two decades. For 'sustainable future', I rely on the projections provided by the Global Deal for Nature, The world in 2050, World Economic Forum, and the *Niti Aayog* (2017), where urbanization is prevented, agricultural productivity is retained, forest browning, coal mining and drying water streams are prevented after 2030, invasive plant management is doubled and climatic changes are prevented (RCP 2.6). I used the invasive plant occurrences from the year 2010 and projected their distribution to the year 2018, which was validated using the observed data in 2018. For eight out of eleven invasive plants, projection was

on average 5865 (SD 7530) km^2 less than the observed distribution, thus providing a conservative estimate.

Distribution of all invasive plants under the business-as-usual scenario was consistently higher as compared to sustainable future scenario. When only climatic changes were considered, 88% of forest was likely invaded in 2050 as compared to 82% forest under the sustainable future scenario. While, when all the landscape drivers were considered for the year 2050, 'business-as-usual' scenario resulted in 96% forests being invaded as compared to 93% forests under the sustainable future scenario. Projections suggested that least invasion was observed in the Northeastern hills. The present study results demonstrate that by curbing mining in the central Indian landscape, at least 42000 km^2 forests could be saved, which could be else invaded by different invasive plants, mostly *Lantana camara, Senna tora,* and *Hyptis suaveolens.* Similarly, a consistent high invasion in savannah was due to the agricultural productivity enhanced by irrigation plans under any future scenarios. This in particular facilitated invasion of *Prosopis juliflora*, *Senna tora, Parthenium hysterophorus* and *Xanthium strumarium.* Fire and loss of water facilitated the invasion of *Ageratina adenophora*, *Chromolaena odorata* and *Mikania micrantha* in the Shivalik-Terai landscape and moist forests of the Western Ghats. Currently, around 98,000 INR is required for managing invasive plants at 1 km^2. And around 24 crore INR is projected to be spent for managing invasive plants every year. However, even doubling the management sites and cost, did not significantly reduced the spread of invasive plants. This indicates the necessity to change the selection of management sites from current ad hoc selection to an evidence based site selection, that can maximize the control of invasive plants in an area.

8. Present study provides national scale estimates for spread of all priority invasive plants. More than 79% forests are presently invaded by the high concern invasive plants at varying degree, and they will likely invade more than 90% by the year 2050. The key drivers were

nearness to invaded sites, urbanization, degrading and drying moist forests, and greening and water supplementing dry forests and savannah. Doubling the cost and area with current management practice was shown to be insignificant in arresting this invasion. Invasive plants tend to expand around sites that are already occupied, and putting efforts to manage the edges to contain spread of invasive plants on priority sites can help reduce the spread in adjoining areas. With current policies, protected areas have lower urbanization influence and higher management actions. Thus, they could be the priority for systematic large-scale control of invasive plants, which will reduce their spread in the adjoining areas. However, savannah and dry forests remain predominantly outside protected areas with a need of alternate management regime. Based on the study results, negative effect of fire on invasive plants can be considered for further experimenting control strategies in these areas.

Interpreting the adaptive responses of invasive plants in the framework of 'niche plasticity', this thesis substantially contribute to the existing niche theory. This is particularly important, as few studies considered that with ongoing climatic changes, niche area of invasive plants might reduce, I show on the contrary. Furthermore, my thesis contribute to the technique of species distribution modelling by providing a way for inter-scale ensemble modelling. We demonstrate how in the name of the tiger, AITMP not only conserve the tiger alone, but can also help conserve its ecosystem. India's invasive plants monitoring program is mandated for future continuation by the Government of India under the AITMP. Presently, many Southeast and South Asian countries use tiger as a flagship species for conservation, but lack inclusion of habitat monitoring. Thus, similar studies could be replicated in countries seeking cost-effective, holistic, inclusive and timely evidence on changing landscapes to invoke adaptive management. It will not only help these countries to keep a tap on their habitat quality but also help achieve the global AICHI targets (target number 9) under the Convention on Biological Diversity's (CBD) Strategic Plan for Biodiversity 2020; and beyond.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: EPISTEMOLOGY OF INVASION ECOLOGY

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"There cannot be both opinion and knowledge of the same thing at the same time."

-Aristotle, Translation from *Analytica Posteriora*

Introduction

The process of 'defining' is a crucial part of critical thinking because it deals with the most fundamental categories of human thought and perception - the categories of similarity and difference. Biological invasion! What rings a bell in mind? Metaphors like 'alien', 'noxious', 'outsiders', etc. that carry an innate sense of wrongness (Chew & Laubichler 2003). Popularly, an invasive species is defined as a wide-spread non-native species that has negative impact on a native ecosystem. Owing to the subjective *differentia* like 'non-native' and 'negative' in the definition, invasion ecology has been criticized for its ambiguous nature (Peters 1991). Although, these terms refer to biogeography and effect on non-human systems, their rationalization is influenced by human perceptions (Richardson et al. 2000). When a term that explains a phenomenon is influenced by human perceptions, it can overtake the rational understanding and conceptualization; particularly in a value-laden aspects of conservation (PySek 1995). Studies have argued that such innate wrongness might help to manage the harms caused by an invasive species. But, cognitive linguists flag that such value-driven metaphor can trigger the extended thought process with imminent compromises on perceptions and facts (Lakoff & Johnson 1999).

Since the notable mention of invasive species by the 19th century scientists, including Alphonse De Candolle, Charles Lyell and Charles Darwin (though not using the same term), there have been efforts to rationalize the definition of 'geographies' and 'effects' in the definition. It is the idea of 'otherness' that has persisted in each of these ideas and identities. As a result, scholars tried to make a value-neutral definition (e.g.(Colautti & Macisaac 2004)) of an invasive species by trying to eliminate the human perception. However, owing to its popularity, value-driven metaphors and adjectives are retained in invasion ecology (MacIsaac et al. 2011). Due to influence of such metaphors on conceptualisation in ecology (Davis 2009), invasion ecology has been recently seen in the larger social milieu of values and politics, and the 'wrongness' or the 'rightness' of biological invasion has been vehemently debated. Opinions of scholars regarding the identity of invasive species are divided into two visible groups, one proclaiming the value-neutrality of invasion science (Holle & Simberloff 2005; Richardson & Ricciardi 2013) and another questioning the necessity of value-neutrality (Brown & Sax 2004; Davis et al. 2011; Schlaepfer et al. 2011). These extreme opinions highlight the importance of a question that the subject must raise: how strong is the science - value interface in invasion ecology and why?

Here, I explored the influence of societal value in development of the concept of invasion ecology. Resisting the temptation to accept invasion ecology as value-neutral science, I've reviewed multiple narratives about the epistemology of biological invasions and subsequently highlighted the necessity of interdisciplinary philosophies in the subject.

Weed and Weediness (Before 15th century)

The earliest known concept of invasive species was regarding plants that affected food resources of primitive human societies as weeds. Weeds and weediness are two ideas that have been constructed since the start of agriculture (Clayton 2003). With the advent of agriculture, the people-nature relationship changed. Any species that damaged cultivable 'good species' were identified as 'bad species' (White 1975). It was not until the biblical ages that weediness was used as a metaphor for representing anything evil and 'unnatural'. Genesis (3:18) states Adam to be cursed with weeds (Speiser 1964), suggesting weediness to be equivalent to something evil (e.g. "*The one who sowed the good seed is the Son of man. The weeds are the sons of the evil one, and the enemy* *who sows them is the devil.*" Matthew 13:33). Because of biblical supremacy, contemporary scholars raised concern for the lost innocence by condemning the 'unnatural' weeds as its cause. This influence always persisted with the term and was even referred by Shakespeare, a scholar of Renaissance Europe ("*this (*world*) an unweeded garden…*". Hamlet 1.2.6).

The theological overtone of unnaturalness in weeds was questioned by different philosophers (e.g. Heraclitus, Zeno of Citium, and Plutarch). Such ideas challenged the dichotomy of 'natural' and 'unnatural' since historic times. These voices were heard with the fall in biblical supremacy. But the visible arguments were due to the growing global connectivity of European scholars during the Renaissance, particularly with the eco-centric oriental societies, who influenced the redefinition of human-nature relation (Kelly & others 2012). The scholars during the Enlightenment era found otherness of weeds to be an outcome of human artifice (King 1957). For example, in the 18th century, botanists argued that weeds were not the cause, but rather, an effect of soil impoverishment. Many post-Renaissance scholars, including Wolfgang Goethe and Russell Lowell, romanticized weeds as 'wilderness that rebelled against human regulation' (Clayton 2003). However, the majority of society was still driven by biblical supremacy that treated few species as innately evil and supported the dominance of what they considered as good species.

Exotic Introduction (1500 to 1900 AD)

Scholars influenced by the idea of European supremacy over others took the advantage of biblical references. For example, Sir Matthew Hale (1667), an English barrister, stated that man is superior to nature and hence must have control to change it (influenced by "*Thou hast given him dominion over the works of thy hands; thou hast put all things under his feet*" Psalm 8:6) (Clayton 2003). Similarly, Raynal (1713-1796), a French writer, believed that modifying wild nature to a garden was what distinguished civilized Europeans from uncivilised Indians (Gilderson 1996). Nevertheless, with the growth of the positivist movement in Europe, science was advocated for any political decision and was reflected by the arguments of scholars advocating species introductions. For example, Walter Buller, a 19th century naturalist from New Zealand, invoked Darwinism for the displacement of native flora and fauna (including people) by superior European species (Clayton 2003). This attitude of 'European gardens better than wilderness' was further backed by the vast improvement in navigation technique and diversity of available modification tools, which helped in transferring the species across the globe and modifying the native biota for economic and political purposes. Amidst the positivist movement, using science for justifying species transfer during the imperial era was thus biblical rooted and was enhanced by capitalist mercantilism and the navigation technology (Beghin & Potier 1997; Hulme 2009).

The transfer of crop plants out of their native areas was an important step in world history, as it facilitated the expansion of societies and empires (Peretti 1998). Most of the non-European societies, particularly Oriental and native Americans were constrained to using and breeding the available species in their area (DiZerega 1996; Kalland & Persoon 1998). However, colonial rule tried to modify the new countries by introducing exotic species, to make the ambience depict their homeland (e.g. introduction of oak, pheasants and rabbits in New Zealand (Wells 2006)) and for economic resources (e.g. introductions of *Prosopis juliflora* in South Africa (Bennett & Kruger 2013)). Perception of native people to such introductions was varied. People fascinated with the imperial lifestyle tried to accept the changes. Those who revolted against the rule led to the movement of conserving the native values and biota. Hence, 'exotic' was used both, as a metaphor for appreciating a unique difference, as well as for criticizing an alien entity.

Nativism (1900 to 1950 AD)

Few of the introduced species escaped in the wild, spreading at an alarming rate and outcompeting the native cultivable and natural species. As a response to this damage, farmers and forest managers started removing such species. For example, Noxious Weeds Act (1900) was established in New Zealand to eradicate harmful introduced species (Chapin et al. 2010); and *Lantana camara* (introduced species) management was initiated (1912) in parts of India (Bhagwat et al. 2012). An extreme version of this idea was to remove any entity that didn't belong to the political extent of a particular society; an idea that led to biotic nativism. 'Native', before the nineteenth century meant anything that was not a direct output of human artifice (Chew & Hamilton 2011). It was later related to the purism of landscape; and such purism was perceived to be free from any foreign invasions. As species were segregated based on the political boundaries and the human race in it, biological nativism was historical outcome of apartheid cultures. For example, in pre-World War II Germany, strict biological nativism was supported by Nazism. Ideologically and ecologically, the Nazis attempted to purify their nation and nature, by eliminating people and biota that were supposedly non-native (Peretti 1998). For example, Reinhold Tuxen, head of the Reich Central Office for Vegetation Mapping, announced fight against the 'Mongolian invader' *Impatiens parviflora*. Such decisions converted wilderness into 'natural gardens', as all the ecological selections were controlled and manipulated by human interventions (Pollan 1994).

Scholars suggest that the emergence of biological nativism could also be a product of newly emerged, democratic, less-developed countries, who suffered due to (political) invasions during the World War II (Peretti 1998; Nunez & Pauchard 2010). The approach adopted by such countries usually relies on eradicating non-native species based on political boundaries. Not surprisingly, the Leopold Report (1963), a scientific document to manage national parks in the United States of America, stated that management should aim to protect and recreate native nature that was present before invasion and degradation by the first white man and biota brought by them (Hecht & Cockburn 2010). Such perspectives were based on a myth of an idealized primitive society living in harmony with the environment (Katz 2014).

Although environmental purism is not inherently racist, there are compelling arguments that nativist purism is undesirable in all spheres-political, cultural and ecological (Peretti 1998). Species ranges and extents are driven by how far they can disperse and how far back in time they did so; political boundaries are proximate, ever-changing and artificial and do not match up with the time scales at which species ranges expand. Hence, political boundaries should not be considered for assigning species with their identities. All the same, contemporary attempts to preserve differing cultures and small-town community life by limiting foreign influence need not be racist or xenophobic, but rather, an attempt to preserve the spectacular diversity on earth (Hettinger 2001). However, if human modification of ecosystems is left unchecked for natural selection to happen, it will lead to the completely human controlled ecosystems (Katz 2014).

Biological Invasion (1950 onwards)

The experience of few species being harmful for the ecosystem, their geographic identities, need to control their impacts and emerging quantitative ecology of 20th century led to rationalization of the concept of biological invasions. The species out of their geographies were recorded by naturalists of 18th and 19th century including Pehr Kalm, Alexander Humboldt and many others (Davis 2009; Chew & Hamilton 2011). Charles Darwin considered this phenomenon, when he observed that non-native species could threaten native species on islands (Darwin 1859). As described by previous study (Davis 2009), the influence of geographies on species was also motivated by Wallace's six distinct bio-regions of earth that inspired the contemporary biogeographers to explore the biology of species outside their bio-region. To geographers and voyagers of the 19th century, this was all about human introductions that affected the species of distinct geographies. One of the first few published record of invasive species, was for species (native or non-native) that burgeoned, resulting in the rarity of other species (Brandis 1891). Subsequently, ecological knowledge accumulated as a product of geological and naturalists' expeditions. Early ecologists observed the ecological difference brought by the species that got out of its native area (Spalding 1909; Thomson 1922; Egler 1942). The impacts that these species can have on the introduced area started getting the attention, particularly with non-native plants (Campbell 1926).

It was not until the 1950's that the subject gained ground in the scientific community. Marston Bates (1956) in his chapter, 'Man as an agent in the spread of organisms', reported that the species which spread with human movement can become 'Neobiota' in different regions (Bates 1956). Another contribution was by Charles Elton (popularly known as the father of invasion biology) in 'The Ecology of Invasions by Animals and Plants'(Elton 1958). Elton flagged the concern on biological invasions using radio broadcast and used general language to convey the seriousness of the topic. Unlike many other scientific publications by Elton, the starting paragraph of his book 'The Ecology of Invasions by Animals and Plants' dramatically claimed "*It is not just nuclear bombs and war that threatens us. There are other sorts of explosions, and this book is about ecological explosions*". Based on the ecological observations for more than a decade, Elton warned that the loss of biodiversity due to invasive species would be so severe that "*Instead of six continental realms of life, ... there will only be one world......*". Scholars criticized Elton's idea as a product of his martial mindset and language developed by the World War society (Chew 2006). However, Elton's work since the 1930's indicates that his monograph was output of long term ecological observations that lead to the concept of biological invasion in 1958 (Kitching 2011). Although, Elton's idea was not influenced by the post-war martial mindset, the society that was habituated with everyday war news could have perceived these martial metaphors literally. And hence, out of two contemporary metaphors of 'neobiota' and 'biological invasion,' it was only the latter that eventually became the highest cited term (Richardson & Pyšek 2008; MacIsaac et al. 2011).

Modern Invasion Ecology (1980 onwards)

Modern invasion ecology that constituted itself somewhere in the 1980s, owes its presence to the advancement in quantitative ecology (Davis 2006). The global awareness for biological invasions was reflected in the SCOPE program (Macdonald & Jarman 1984) that resulted in exponential increase in quantitative data about the spread and effects of biological invasions (Richardson & Pyšek 2008). Association of the impacts with ecosystem services and biological extinctions enabled the subject to gain strength for raising funds and carrying long term research. The post-1980 rise in scientific publication and citations on biological invasions symbolizes a modern rationalization of subject (PySek 1995). As evident from the adjective 'modern', the new version of invasion ecology was based on induction (ecological surveys, lab experiments, etc.) and deduction through statistical hypothesis testing. But the ultimate objective of biodiversity management was to maintain the 'balance of nature' by managing invasions. Definition of the geographies and 'negativity' associated to the identified species is only partially addressed by such modern approaches. Thus, the workable modern definition for an invasive species was - widespread non-native species whose introduction is mainly attributed to humans and which negatively impact the ecological integrity (Colautti & Macisaac 2004). The meaning of 'non-native', 'human induced' and 'negative impact' are left to interpretation by the scholars and the stage of invasion in the ecosystem.

In the modern definition of biological invasion, anthropogenic activity (Hulme 2009) is popularly considered responsible for introducing a species out of its evolutionary range, where it might turn invasive due to a release from controlling agents (competitors, predators and disease). Such assumptions suffer from ecological limitations as one cannot be definitive about the evolutionary history, or about the conservatism of this evolutionary niche of a species (Walther et al. 2002). With increased human transport available, humans are spreading many species out of the geographic barrier, will all these species become invasive? There have been evidences suggesting that distinct geographic origin of a species cannot be the only reason for its invasiveness elsewhere (Davis et al. 2011; Hassan & Ricciardi 2014). Hence, the duration for which a species be present in a particular location to be classified as native is more a philosophical issue (Westman 1990) and then an ecological one. The second criterion of 'negative' impacts was developed keeping in mind that not all human induced non-native species turnout to be harmful. According to this criterion, invasive species are not integrated into the ecological community, but are the ones that degrade it. Recent studies show that natural communities are dynamic and hence, constantly prone to change (Lavergne et al. 2010). Scholars have been challenged with providing a principled distinction between harming a natural system and changing it (Gunn & Throop 2002). When the harm is to a nonhuman system, the justification for negative impact is complex, and scholars have recently proposed to incorporate human-values in the framework of defining negativity of impacts (Jeschke et al. 2014).

Further, as climate change unfolds, species will change their current distributions to survive (Peterson et al. 2002). Will such species then be considered as invasive? It is inevitable that differential changes in any community will lead to the introduction of hitherto unknown species and can even result in them becoming abundant. If I want the natural processes to occur without human intervention, then the ecosystems will be invaded. And if I intervene, the processes will be no longer 'human-free'; this alarms the onset of Anthropocene (Fritz et al. 2003; Steffen et al. 2007).

Contemporary Invasion Ecology (2010 onwards)

With the fall of Clementsian concept of climax in modern ecology, thoughts began to appear that challenged balance-of-nature paradigms regarding ecosystems. Invasion ecology, as a subject, has evolved from the normative binary of 'good' and 'bad' species, to a modern thought of abrupt state of ecological equilibrium. The upsurging era of postmodernity (Lyotard 1984) is questioning the 'balance of nature' and perceiving it as multiple states based on chaotic processes (White 1998). Postmodernity, as a state of society, might be yet debated but, increased references of chaotic processes in ecology (Evans et al. 2013) and the new paradigms of multiple stable states (Fukami & Nakajima 2011) allude to a common reference of postmodern thoughts in ecology. An ecosystem is now perceived as a dynamic response to the changes in the environment, explanation of which can be found elsewhere (Scheffer & Carpenter 2003; Hobbs & Norton 2004). This criterion does not weigh the geographic origin of a species or negativity of its impacts as important. The first important factor is the potential regime shift in a non-ecological time and second, the anthropogenic base of such shifts.

The alternate stable state is a product of human manipulation of the ecosystem, in an era of biodiversity crises due to anthropogenic influence, and thus it induces concern. Secondly, biological invasions claim to accelerate biological extinctions and economic loss (e.g. loss of US$ 314 billion per year for six nations (Pimentel et al. 2001)), and hence could be perceived as a risk (Burgman 2005). However, the potential alternate stable state poses an interesting conundrum for managerial action, as removing an invader from the new regime of the ecosystem can disturb the newly established ecological networks and processes. This loss of interaction could further move the system into other chaotic states (Hughes et al. 2013). Reverting back the ecosystem to its pre-invasion state, which in itself is subjective, needs control on all micro-parameters of the ecosystem. Moreover, waiting for an ecosystem to cross the existing regime and then reverting it back consumes resources with uncertain ecological gain. The way science can help is by providing early warning signals of ecological regime shift by biological invasions, so that strategies to resist it or adapt to it, could be timely availed.

The contemporary conservation strategies propose restoration of lost ecological regimes rather than only removal of invasive species. Owing to small sizes of protected areas and human influence on its ecology, the probability of ecosystem reverting back to its original regimes on its own is miniscule. Although, humans would regulate transformation to such a system, thereby making it anthropogenic selection; it would minimize the relative damage caused to the biodiversity. The current postmodernist views, alluding to their placement of human as a part of nature will support interventions in such cases (Robertson & Hull 2001), but should be freed from the xenophobic base. There is an urgent need to modify certain thoughts to compliment scientific decision in dealing such conservation strategies. Many conservation biologists emphasize the importance and pervasiveness of species migration while maintaining a nativist ideology (Peretti 1998). This clash, many a time, has resulted in deactivating the management of some harmful invasions, while sometimes having resulted in removal of native species (Sagoff 2000) and has also ended up terming threatened species as exotic and alien (e.g.(Thapar 2013)). Secondly, conservationists often target species that have visibly altered the landscape to an extent that adaptation to the change is costlier than removing the species. Such dissonance could be overcome by multidisciplinary studies that have already been demanded (Larson et al. 2011).

It is a time where, scholars from ecology, sociology and quantitative science come together to address the conceptualization and actions regarding biological invasions. Multi-disciplinary initiatives are showing success in using value-judgements without influencing the scientific premise. For example, considering opinions of the animal rights group resulted in successful control of feral pigs in Texas USA (Peterson et al. 2011), public participation for controlling invasive plants spread in Australia. Invasion, in its entire context is part of ecological science and not a different science in itself as indicated by few. Science in its positivist form is inept to solve such problems alone as "*meanings cannot be measured, only understood*" (Bhaskar 2014). Meaning could be multi-narratives and should not be feared; as our study demonstrates - including the contradictions in existing views, environmental conservation has always been a heterogeneous mixture of ecology, politics, sociology and culture.

CHAPTER 2: SYSTEMATIC REVIEW ON BIOLOGICAL INVASIONS IN INDIA

Part of the chapter was published as a peer-reviewed publication: Mungi NA, Kaushik M, Mohanty NP, Rastogi R, Johnson JA and Qureshi Q (2019) Identifying knowledge gaps in the research and management of invasive species in India. Biologia 74(6): 623-629 https://doi.org/10.2478/s11756-018-00186-8

Introduction

As a developing nation, India has recently accelerated its developmental projects for economic growth (GDP of $8998.6 billion Purchasing Power Parity (World Bank, 2018)). Most of the ecosystems in India are under a gamut of anthropogenic influences, which might facilitate invasive species and affect already threatened native species. Furthermore, invasive species have hampered ecosystem services and associated economics of the country. The total cost of environmental and agricultural loss caused by the invasive species in India is speculated to be around 116 billion USD per year (Pimentel et al. 2001). As a result of increasing concern on biological invasions, India included invasive species management as its fourth target of the Fifth National Report to the Convention of Biological Diversity, stating "*by 2020, invasive alien species and pathways are identified and strategies to manage them developed so that populations of prioritized invasive alien species are managed*". India has an estimate of approximately 225 plants species that are non-native (Khuroo et al. 2012). However, managing all these potential invasions by 2020 is neither practical nor essential. Successful invasive species management elsewhere, has demonstrated the importance of species prioritization, leading to effective allocation of resources (Koehn & MacKenzie 2004; Nel et al. 2004). Hence, selected few High Concern Invasive Species (HiCIS) with known negative impacts were focused for management through an expert panel comprising of stakeholders involved in research and management of invasive species in India (Mathur et al. 2015).

However, a systematic prioritization using information on invasive species ecology and their management aspects is missing; nevertheless, few invasive species has been managed by different stakeholders in almost all landscapes and major ecosystems of the country (Bhagwat et al. 2012). These experiments and their results are restricted to the regional reports and practice guidelines (i.e. forest management plans and habitat restoration reports). Hence, it is essential to also include this grey literature in addition to peer-reviewed publications for filling the knowledge gap for robust prioritization. Such review-based prioritization is usually conducted by using two frameworks 1) Evidence-Based Analytical Protocols (Morse et al. 2004) and 2) Expert-Based Evaluation Protocol (Robertson et al. 2003; Liu et al. 2010).

Evidence-Based Analytical Protocol relies on scientific experimentations and logic-based criteria to identify a species as high concern invasive. This is the most efficient way to develop precise information about non-native species and rank their management based on the ecological and economic threat. It usually includes life history strategies, effect on components of native ecosystem, distribution status, and policies on invasive species management. The major drawback of this approach is its time and resource exhaustive nature (Randall et al. 2008). Expert-based evaluation protocol uses similar set of criteria to rank invasive species management based on the field experience and/or subject knowledge. It includes interviewing experts with different stakes in the subject for information on their perception and experience of managing high concern biological invasions. Major limitation of this approach is its value-driven nature and subjectivity regarding the ranking system (Kumschick et al. 2012). However, both approaches can be used in combination to overcome the limitations and improve the timely decisions and its effective outreach. This process also helps to bridge the gap between managers and scientists by bringing them on the common platform for the assessment (Lach et al. 2003; Marris 2006). Present study relies on this combination of methods.

In the study, I reviewed existing knowledge on the HiCIS in India by using a prioritization framework. I evaluated all these HiCIS for available knowledge on their ecology, impacts, and management. Subsequently, I synthesized information critical to the management of these invasive species, identified knowledge gaps, and provided flexible prioritization options. Furthermore, I examined the correlation in individual criteria and priority score for testing if the identification of an invasive species as HiCIS, by expert panel, is valid scientifically. The study aims to aid in achieving the 4th national biodiversity target of managing invasive species by 2020.

Method

I used 21 species in four major ecosystems viz., terrestrial, fresh water, marine, and island ecosystem that were identified as the HiCIS (Mathur et al. 2015). For each species, I reviewed studies under three modules - ecology, impacts, and management, for assigning the priority scores using the Delphi method (Robertson et al. 2003). Under this framework, each module had multiple criteria which could be quantitatively scored. The ecology module had criteria evaluating species distribution, density, dispersal, dispersal agents, invasiveness, and recolonization potential. The impact module had criteria regarding species' impact on biodiversity, physical parameters, ecosystem services, and economics. The management module had criteria on controlling techniques, restoration, legislation, stakeholders, and conflict involved. Thus, in total 21 species were evaluated for 17 criteria under three modules.

I conducted a literature search using ISI Web of Knowledge database and Google Scholar. The publication period, journal categories, and languages were not restricted. Species name and generic synonyms (e.g., *Cassia tora* OR *Senna tora*) were used as the search string for finding relevant information on every species. My study was focused on the criteria published in Mungi et al. 2019, and hence, I avoided any literature regarding phytochemical analysis, behavior, animal husbandry, disease pathology, and impacts and management related study outside the political boundary of India. A separate review was conducted to collate species-specific information on traits (Mungi et al. 2015, unpublished information). The criteria under the ecology and impact modules of species are usually studied and published. However, excluding few popular invasive species, I rarely found the criteria for management module scientific publications. Hence, I collected information from managers and other practitioners in the aforementioned workshop, regarding different techniques used across the country and the associated economics, legislation, and stakeholders involved.

Each criterion was scored using the existing scientific knowledge and expert opinion to derive a priority score. Scoring for each criterion was either binary or ordinal. Therefore, the priority score was higher for species with established ecological information regarding its distribution, dispersal and impacts on ecosystem as well as inadequate information on management. To standardize the precision of information obtained from varying sources, I included an associated confidence score. If the criterion score was based on published evidence, the confidence score was 1; if based on unpublished data (i.e. grey literature) or experience, it was 0.5; and if based on extrapolative interpretation of studies, it was 0.25. Confidence scores not only represent the precision of criterion scores but also indicate the state of knowledge about each species.

After assigning criterion and confidence scores for every species, the summed score for every criterion was standardized by dividing it with the maximum possible score for each criterion, to make all criteria comparable. I further developed four priority models namely neutral, management prioritized, impact and invasiveness potential models by assigning different weights to every module. Neutral model: assigning equal weight to all module; whereas, in other models, higher weight was given to the module of interest while assigning equal weight to rest of the modules. This weighting scheme provides flexibility and control to the decision maker to choose priority based invasive species as per their focus and demand. In case, the stakeholders are interested in managing invasive species with existing guidelines on management techniques and policies, management model can be used to identify such HiCIS. In another case, if decision makers are concerned about the high impact on native species due to an invasive species, they can use the impact model.

I calculated module confidence score by summing the confidence score and dividing it by the total number of criteria in a module. The final priority score was obtained by summing the weighted module scores and its confidence for each species. I ranked species based on this priority score and associated confidence scores. Different ecosystems were compared for differences in priority and confidence score by using Mann–Whitney *U* test. Subsequently, I correlated the overall priority score generated by the neutral model with standardized score of all criteria (e.g., effect on biodiversity, availability of policy for management or control, etc.) of every species using Pearson correlation and assessed its statistical significance. It identified the factors responsible for perceiving a species to be a high priority.

Result

Out of 14 HiCIS plants, one was an algae and 13 belonged to dicotyledonous class of angiosperm. Of the seven HiCIS animals, one was mollusk, four were fishes, one was amphibian, and one mammal. Overall, priority score of freshwater ecosystem was higher, but statistically insignificant ($p < 0.50$) compared to terrestrial ecosystem (figure 1). However, confidence scores of terrestrial ecosystems were significantly higher ($p < 0.004$) to freshwater ecosystem. When assessed between terrestrial and island ecosystem, terrestrial ecosystem had higher priority, though statistically insignificant ($p < 0.11$) and significantly higher confidence score ($p < 0.05$) respectively (figure 1). Out of all the criteria considered, a significantly positive correlation with the neutral priority module was observed for criteria on impact on biodiversity ($R = 0.63$, $p < 0.005$), impact on physical environment ($R = 0.70$, $p < 0.005$), and impact on ecosystem services ($R = 0.60$, $p < 0.01$); while significantly negative relation ($R = -0.46$, $p < 0.05$) was observed with availability of legal instruments. A marginally significant positive correlation was observed in the neutral priority score and the criteria of spatial distribution ($R = 0.42$, $p < 0.1$).

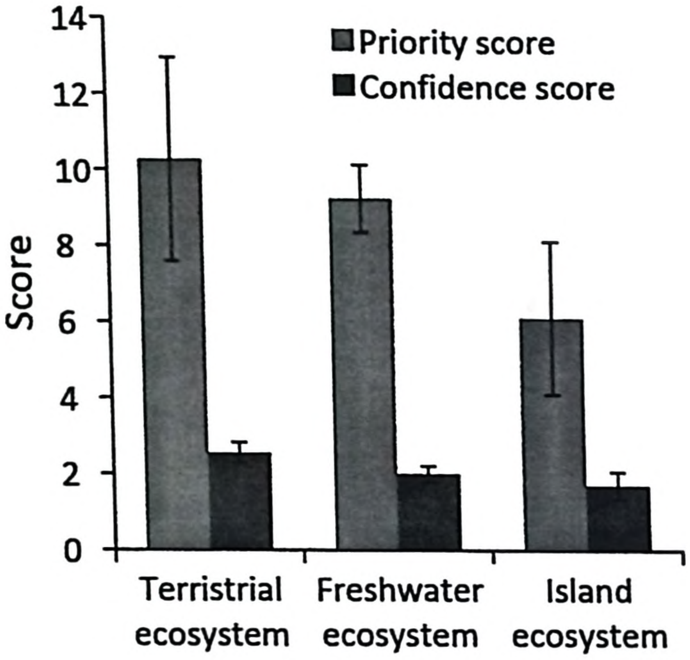

Figure 1 Comparing priorities of ecosystems: Averaged priority and confidence scores (mean ±SE) for High Concern Invasive Species across different ecosystems (Marine ecosystem was excluded as it had only one High Concern Invasive Species, which cannot be compare using present statistics)

Terrestrial ecosystem had 11 plants and one animal identified as high concern by the experts during the workshop. Prioritization framework identified *Prosopis juliflora* as the top HiCIS priority followed by *Chromolaena odorata;* whereas, *Xanthium strumarium* and *Ageratum conyzoides* gained the least priority across all priority models (table 1). *Parthenium hysterophorus* was the species with the highest confidence score across the ecosystems; while, *Xanthium strumarium*, *Ageratum conyzoides* and *Hyptis suaveolens* were the species with the least confidence in the terrestrial ecosystem (table 1) (figure 2). Giant African land snail *(Achatina fulica*) received higher priority in management weighed model and had moderate confidence score (table 1).

In island ecosystem, populations of Spotted deer (*Axis axis*) and Indian bullfrog (*Hoplobatrachus tigerinus*), occurring on the Andaman Islands, received higher priority. Spotted deer received higher priority score (figure 2), as well as confidence score than the Indian bullfrog (table 1). Spotted deer also had higher criterion and confidence score across all priority models (table 1). Spotted deer ranked higher in management model as compared to ecology and impact models. Indian bullfrog was ranked the lowest among all species.

The freshwater ecosystem had the second highest number of priority species after terrestrial ecosystem. Four fish and two plant species were identified as HiCIS in freshwater ecosystems. Prioritization framework assigned highest priority and confidence score to *Eichhornia crassipes* followed by *Clarias gariepinus* in this ecosystem. Interestingly, *Eichhornia crassipes* received lower priority in management module, whereas, *Clarias gariepinus* received highest priority (table 1). *Cyprinus carpio* had least priority and confidence score across the models in the ecosystem, followed by *Ipomoea carnea*, which was the second last in the category; both with moderate confidence score. *Oreochromis mossambicus* was a species with moderate priority and confidence score (figure 2).

The sea algae *Kappaphycus alvarezii* was the sole nominated marine invasive species by the experts attending the workshop. The algae ranked seventh in management weighed model; else, it ranked at the ninth amongst all the HiCIS (table 1) (figure 2).

Discussion

Terrestrial mainland ecosystem had the highest number of HiCIS, whereas, the marine ecosystem had the lowest. Confidence score, representing the accuracy of the derived priority scores for the given HiCIS, was also highest in the terrestrial ecosystem pointing towards higher degree of scientific consideration. Nomination of a single species in marine ecosystem, though, reflects scantiness in research about marine ecosystem; but it might also be a product of under representation of experts in the panel identifying the HiCIS (Mathur et al. 2015). Similarly, previous studies have also expressed the paucity of information regarding invasive status of fungi, bacteria and other microorganisms (Bebber & Gurr 2015). Though their impacts on human modified landscape in India (e.g. agricultural field, pisciculture, and animal husbandry) are established (Pimentel et al. 2001), information about their status and control mechanism is limited.

Table 1 prioritizing invasive species: Priority scores of High Concern Invasive Species (HiCIS) under different priority models based on their ecology, impacts, and management. Degree of red represent increasing priority. Confidence score represent the quality of existing scientific knowledge for every species.

Species name	**Neutral model**	**Management model**	**Impact model**	**Ecology model**	**Confidence score**
Prosopis juliflora	15.0	9.8	10.2	10.1	2.7
Chromolaena odoratum	12.7	8.5	8.4	8.8	2.8
Mikania micrantha	12.1	7.8	8.3	8.5	2.7
Parthenium hysteroporus	12.1	8.0	8.0	8.6	2.9
Mimosa diplotricha	12.1	8.1	7.9	8.5	2.8
Lantana camara	11.7	7.4	7.7	8.5	2.7
Eichhornia crassipes	11.0	7.0	7.4	7.8	2.7
Clarias gariepinus	10.4	7.3	6.7	7.1	2.2
Kappaphycus alvarezii	10.1	7.6	6.2	6.9	2.4
Salmo trutta fario	9.8	6.8	6.0	6.8	2.0
Senna tora	9.5	6.4	5.6	7.1	2.4
Oreochromis mossambicus	9.2	6.5	5.7	6.4	2.1
Ageratina adenophora	9.0	6.2	5.7	6.5	2.4
Ipomoea carnea	8.6	6.2	5.5	5.9	2.1
Cyprinus carpio	8.2	5.7	5.2	5.7	1.7
Hyptis suvavolence	8.2	5.8	5.0	5.9	2.2
Axis axis	7.5	6.0	4.9	5.0	2.0
Achatina fulica	6.9	6.3	4.4	4.5	2.4
Ageratum conyzoides	6.7	5.4	4.1	4.6	2.1
Xanthium strumarium	6.5	5.6	3.7	4.6	2.2
Hoplobatrachus tigerinus	4.7	3.9	3.0	3.1	1.5

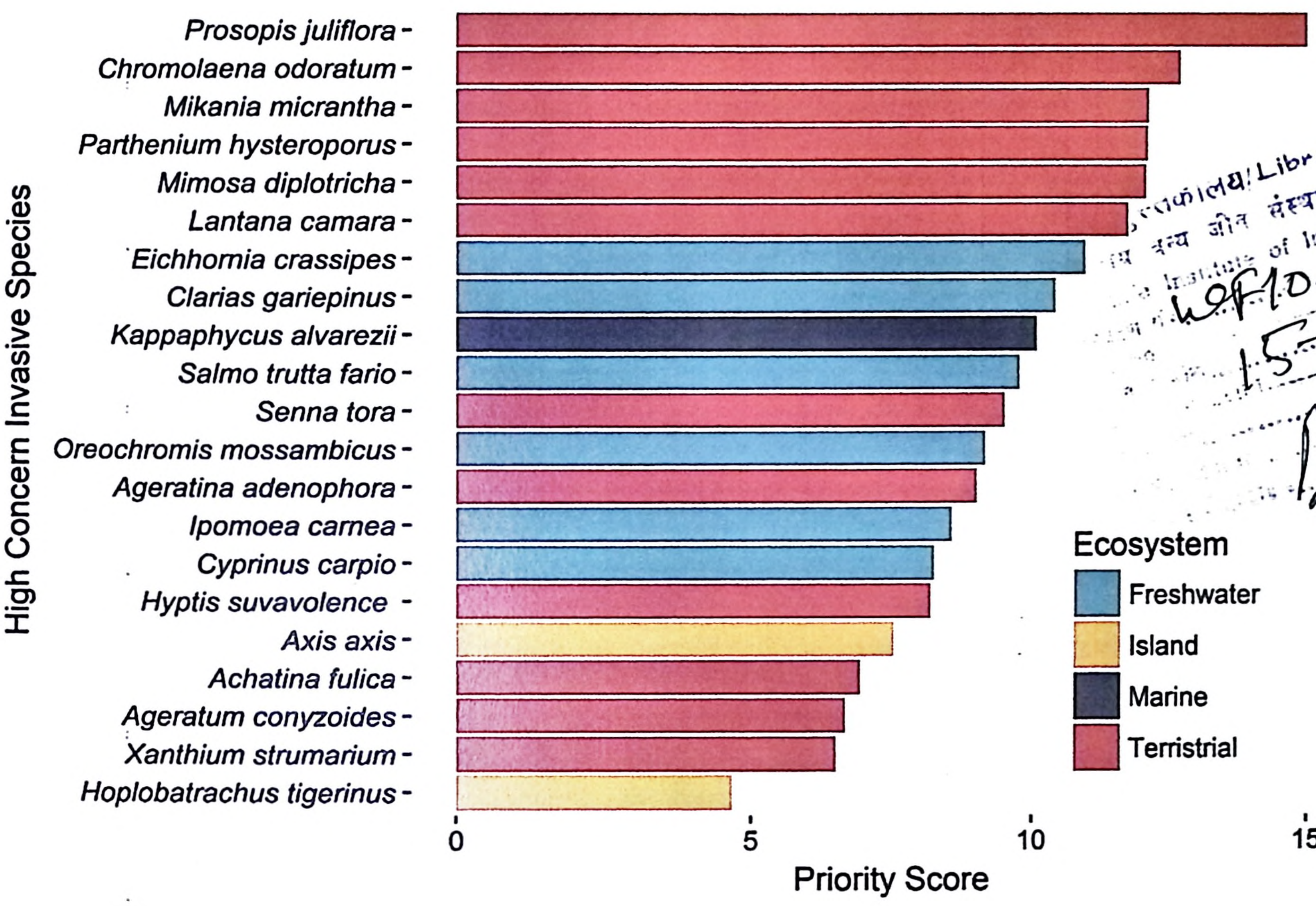

Figure 2 Prioritizing invasive species: Priority score of High Concern Invasive Species (HiCIS) across different ecosystems

Lastly, one major lacuna of this review was exclusion of the effects of climatic changes on invasive species. As India prepares for revolutionary development that comes with extensive land-use changes, global and regional modifications are bound to expand invasive species. But there is no study demonstrating the effects of these changes on HiCIS, the only studies on climatic changes are based on correlative niche models that weighs less credibility to species ecology. Contrastingly, higher confidence score (i.e. established evidences) in terrestrial ecosystem reflects the bias in research across ecosystems. Due to differences in the conservation priorities and ecological settings of these species and ecosystems, each ecosystem needs separate consideration and is published (Mungi et al. 2019). Here, I restrict the discussion to terrestrial ecosystem.

Terrestrial invasive species were the most addressed invasions owing to the threats they pose to the flagship species in mainland India. The top priority invasive plants (*Lantana camara, Prosopis* *juliflora, Parthenium hysterophorus, Mikania micrantha* and *Chromolaena odorata*) are spread across different biogeographic zones of the country. Management programs like biological and integrated mechanical control were used for controlling these species, but were scarcely followed by long-term management and restoration (Bhagwat et al. 2012). *Mimosa diplotricha* is regionally abundant in North-Eastern India and pose a threat to the grassland ecosystem that inhabits source population of the Great one-horned rhinoceros (*Rhinoceros unicornis*); hence, its management has been recently prioritized. Relatively less priority invasive plants (*Ageratum conyzoides, Ageratina adenophora, Xanthium strumarium, Hyptis suaveolens* and *Senna tora*) are known to be abundant in grasslands, savannahs, and along riverbeds. As evident from their moderate confidence score, there is a gap in information on their ecology and management. Although, mechanical removal is used to remove these species temporarily, it is ineffective as they re-invade the area in the longer run. Thus, plant removal followed by restoration of native habitats is of prime importance for cost-effective management for all the invasive plants but has hardly been followed. The only animal researched for its invasion in this ecosystem, Great African land snail (*Achatina fulica*) had an information lag on its management. Hence, all the species in this ecosystem had established invasiveness and yet lack explicit management or management orient research, particularly on providing models of distribution and parameters influencing it.

As India plans to manage the priority species by 2020, it is crucial to focus on management research, as invasiveness and impacts are already documented. The spatial distribution of invasive species often represents invasiveness and provides an opportunity for prioritizing management. However, I observed that the information on spatial distribution for all HiCIS at a scale relevant for management is unavailable, which is crucial for prioritizing management effort (e.g. plants are usually managed at a spatial scale of hectares, while animals are managed as number of individuals). Notably, I found existing legal instruments through which a species could be declared as invasive for managing it inside/outside protected areas. These legal instruments and guidelines for invasive species management were part of larger legal schemes (e.g. National Forest Policy 1988, National Working Plan Code 2014, Marine Product Export Dev. Authority) and wildlife laws for protected area management (e.g. Wildlife (Protection) Act 1972). Given that, the lack of explicit legal scheme and guidelines for invasive species management might bring subjectivity due to differing interpretation of a given scheme by the park managers. It would be particularly true for managing invasions inside Protected Areas that are governed by strict national laws. Nevertheless, our synthesis revealed that invasive species have been managed, in certain cases, under existing umbrella policies and Acts (e.g. forest policies by the state of Madhya Pradesh-2005, Maharashtra-2008, Assam-2004). However, it is legally mandated to prove a species to be invasive and detrimental for the ecosystem, which in turn demands for scientific research and experimentation. Hence, I disagree with previous study (Kannan et al. 2013a) which believed legal unawareness responsible for poor management of invasive species in India, but simultaneously voice concerns regarding lack of explicit schemes for declaring and managing invasive species.

The significant relationship between priority scores and impacts of the HiCIS on native biodiversity, environment, and ecosystem services, explain the significance of impacts on biotic components while identifying a species as HiCIS. Negative relationship between priority scores and lacuna in information on legal instruments for management indicates that only the popular species with high priority have policies and guidelines for management. Hence, identification of the HiCIS through expert opinion holds an ecological parity and scientific validity, which could take longer for systematic research otherwise. Thus, for megadiverse countries, expert opinion could provide a temporary guidance in the absence of scientific research for invasive species identification and management.

CHAPTER 3: RESEARCH DESIGN

"*If there is a creator, ...who surveys it all, he knows or maybe even he does not know*"

-Translation from the *Rigveda*, 10:129

Rationale

While invasive species are spreading at an alarming rate and homogenizing global biota, our knowledge on their status at large-scale remains disjunct, disparate, and often outdated (Delaney et al. 2008). As a result, fundamental information on invasive species spread and theories in invasion ecology are contested for unavailability of empirical evidences (Qiao et al. 2017). Particularly in tropical developing countries, where the potential to conserve biodiversity is higher as compared to developed countries (Early et al. 2016; Barlow et al. 2018), lack of evidence can hinder invasive species management (Matzek et al. 2014). One such example is that of India, a tropical developing country harboring eight percent of global biodiversity that co-occur with highest growing human population in the tropics (16.4 million persons/year) (World Bank, 2018). Unlike other tropical developing countries, where forested areas are reducing to the increased developmental activities, forest area in India was reported to increase at an overwhelming rate over the last decade (1120 km²/year) (FSI 2006, 2009, 2011, 2013, 2015). On the contrary, studies flag that the increase is misleading due to inclusion of plantation and invasive exotic plants as 'forest' (Grainger 2010; Puyravaud et al. 2010). Amidst the controversy of considering invasive plant spread as increased forest cover, marked lacuna in national-level initiatives for assessing invasive plants' spread in the forested areas are impeding timely management actions (Mathur et al. 2015).

In the past, studies have explicitly explored the nature of invasion at local scales and its ecological consequences (Sharma et al. 2005, 2011; Kohli et al. 2006; Tiger et al. 2009; Love et al. 2009; Rana et al. 2010; Hiremath & Sundaram 2013; Ramaswami & Sukumar 2013a, 2013b, 2014, 2014; Kumar & Mathur 2014; Ramaswami et al. 2014; Joshi et al. 2015; Sundaram et al.

2015). Studies have used the presence of few popular invasive species at smaller scale and extrapolated at landscape scale; however, they suffer ecological limitations (Goncalves et al. 2014). Irrespective of the rigorous statistical algorithms, extrapolating the species-environment relation from a small sampled area to a heterogeneous landscape of a mega-diverse country, like India, bears an inherent limitation. The climatic settings, disturbance regimes and socioecological scenarios in India are diverse and unique (Rodgers et al. 1999). Invasive species are known to respond independently to these parameters in different geographies (Mungi et al. 2018). Hence, a country scale sampling for assessing the distribution status of invasive species is essential. Secondly, it is difficult to validate the benefits of such large-scale sampling and ecological changes, without ensuring its repetition (Yoccoz et al. 2001). For a developing country like India, repeating country wide assessment on a regular basis, at an optimal scale, for a specific purpose is resource demanding and would be unsustainable, unless linked with a greater conservation reward.

The Government of India has used All India Tiger Monitoring Project (AITMP) as an umbrella project that ensures the use of tiger's (*Panthera tigris tigris*) charisma to garner resources and public support for securing natural systems along with their functions (Tiger Task Force, 2005). The AITMP protocol is developed to quantitatively evaluate the occupancy and density of flagship animals, habitat quality, and anthropogenic impacts on the forests (Jhala et al. 2006, 2010, and 2013). The protocol for assessing habitat status is used for collecting information on invasive plants by systematic sampling. With an objective of understanding the spread of invasive plants in tropical India, I proposed my study using the information from this large-scale sampling to address the following research questions:

Research Objectives

1. What is the spatial and temporal pattern of plant invasion in tropical India?
    a. Mapping the spatial extent of the high concern invasive plants

    b. Estimating the rate at which these invasive plants are spreading

2. What factors govern the success of plant invasion?
    a. Identifying the drivers of invasions and their influence at multiple scales
    b. Assessing the biogeographic changes in the species' niche
    c. Understanding the changes in species traits across its biogeography

3. What will be the effect of climate change on invasive plants?

In the present chapter, I elaborate India's invasive plants monitoring program, which was repeated four times as an integrated part of AITMP and is mandated for future continuation by the Government of India. Here, I mapped the presence of 11 high concern invasive plants at the national scale and assessed the area under the invasion; which showed that more than 90% of the sampled forests are substantially invaded at an alarming rate, ever known before. It represents globally quintessential sampling efforts for invasive plants; and provides an indication towards deteriorating quality of forests in developing countries like India.

Study area and sampling design

Forested areas were systematically sampled in 18 out of 29 Indian states; this represents 73% of the total forest area in India. Biogeographically, this region is comprised of lower Himalaya, Gangetic plains, Deccan peninsula, Semi-Arid region, Western Ghats, North-East hills and Coasts. Typical monsoon ecology added to the heterogeneous terrain has characterized diverse phytogeography of this region (Mani 1974). These forests are not only the substantial part of India's geography and carbon stock, but also priority habitat of many endangered flagship species like the Tiger. Owing to the massive fragmentation and biological invasions in the habitat of these flagship species, habitat assessment was made an integral part of the AITMP (Jhala et al. 2011).

Sampling design based on virtual divisions (e.g. grids) is statistically suitable; however, identifying a virtual cell in large forest landscape is logistically challenging. Natural divisions that are adapted for administration, law enforcement and biodiversity monitoring, were used. Administratively, the Indian forests are divided in smaller patches called as 'beats'. Boundaries of beats are based on natural features like ridges, waterways and dirt tracks; and a team of guards is deployed for monitoring and protecting the beat. These beats are hierarchically integrated in larger ranges, which are subsequently integrated into divisions, states and country; with every hierarchical class having an additional team to supervise the monitoring and protection of the forest under it. The average beat size in the sampling region was 26.5 (SE 14.8) km^2. As invasive plants differ in their response to micro-habitat (Raghubanshi & Tripathi 2009; Ramaswami & Sukumar 2014), each beat was further divided on the basis of forest types in it. Forest classification proposed by Champion and Seth (1968) was used that divided Indian forests in 103 classes by considering the edaphic characteristics, temperature and precipitation regimes to describe micro-variations in floral communities. Within every substantial sized (>2 km^2) forest type in a beat, the sampling team walked a straight line of 2 km, where at every 400 m three concentric circular plots of 30 m, 10 m and 2 m diameter were sampled. Invasive plants were identified to vary at this scale by various studies in the region (Joshi et al. 2015; Mungi et al. 2018). Within a 30 m diameter plot, plants were categorized by their height to record abundance of tree species (height > 2 m). Canopy cover for each plot was recorded by visually estimating the percent visible open sky from five different locations and averaging it. Simultaneously for each plot, human impacts were quantified as the a) number of trees with lopped branches, b) number of trees cut, c) evidence of grass and bamboo cutting (as present or absent), d) number of people seen from the plot, e) number of livestock seen from the plot and f) livestock-human foot trails within the plot.

1. Within a 10 m diameter plot, percent cover of shrub species (3 m> height > 0.3 m), and invasive/weed species were recorded using a 5-point ordinal scale modification of the (Daubenmire's scale, 1968).

2. Within a 2 m diameter plot, ground cover was quantified by recording a) grass species, b) herb species (height < 0.3 m), c) percentage of leaf litter, and d) percentage of green grass, dry grass, herbs, invasive herbs, and bare ground, which adds to 100%.

The beat guard, who has an intimate knowledge of the forest, participated as a team member to sample plots. Subsequently, few selected plots were sampled by a team of trained biologists. Regional floras (Sharma 1993; Daniel et al. 2005) and photographic guides were used for confirming the plant identification. The survey path and plot locations were recorded using an accurate GPS unit. The survey was repeated four times since its initiation i.e. in 2006, 2010, 2014 and 2018. The total plots sampled in each cycle of sampling, and involved time, human and monetary resources are summarized in Table 2.

Table 2 sampling efforts: Total sampling efforts for monitoring invasive plants and involved human and monetary resources in the year 2006, 2010, 2014 and 2018.

Title	**Year 2006**	**Year 2010**	**Year 2014**	**Year 2018**
Sampled plots (30m diameter)	117,104	132,150	157,121	158,979
Sub-set plots sampled by biologists	2,126	7,341	4,805	-
Sampled forested area (km^2)	169,002	203,810	278,675	162,441

A spatial grid of 5 X 5 km was generated for India in GIS domain, as it matches the size of sampling unit (i.e. beat). The presence of 11 plants recognized as high concern invasive species (Mathur et al. 2015) was attached to a grid cell and mapped. Subsequently, grid cells that were repeatedly sampled in each cycle were used to estimate the forest invaded by each species, and rate of change in invaded area using linear regression.

Primary observations

The sample coverage for every sampling cycle is depicted in figure 3, which represents a coverage of sampling 42% forests in 12 years. Of the total 351,591 km^2 forested areas sampled across India, 76,989 km^2 forests were inside protected areas (National Parks, Wildlife Sanctuaries, Biosphere Reserve, Conservation Reserve and Tiger Reserves), while the rest of it were outside protected areas (reserve forest, eco-sensitive zone, territorial forest, etc.). In the four subsequent cycles, the high concern invasive plants invaded 69% surveyed forest in 2006, 76% surveyed forest in 2010, 80% surveyed forest in 2014, and 83% surveyed forests in 2018. Primary observations regarding the occurrences of these species was made using the references of forest cover map, human disturbance indices and climatic factors; and is compiled in Appendix 3. *Lantana camara* was the most widespread invasive plant across the sampling cycles followed by *Senna tora* and *Prosopis juliflora*. The highest invasion was observed in dense forests (58% of the sampled forests), followed by open forests (53% of the sampled forests), moderately dense forests (52% of the sampled forests) and least invasion was observed in scrub-savannah (40% of the sampled forests). Scrub-savannah was mostly invaded by *Prosopis juliflora, Parthenium hysterophorus, Senna tora* and *Xanthium strumarium*, open and moderately dense forests were mostly invaded by Lantana camara, *Senna tora, Ageratum conyzoides* and *Mikania micrantha*,while dense forests were mostly invaded by *Ageratina adinophora, Chromolaena odorata,* and *Lantana camara.*

An area of 86,700 km^2 was consistently sampled at the scale of 25 km^2 (5932 grids) across the sampling cycles. Within this common sampling frame, 10 species had significantly increased, while one species (*Parthenium hysterophorus*) had significantly decreased (table 3). *Mikania micrantha* had highest invasion rate; followed by *Chromolaena odorata* and *Lantana camara.*

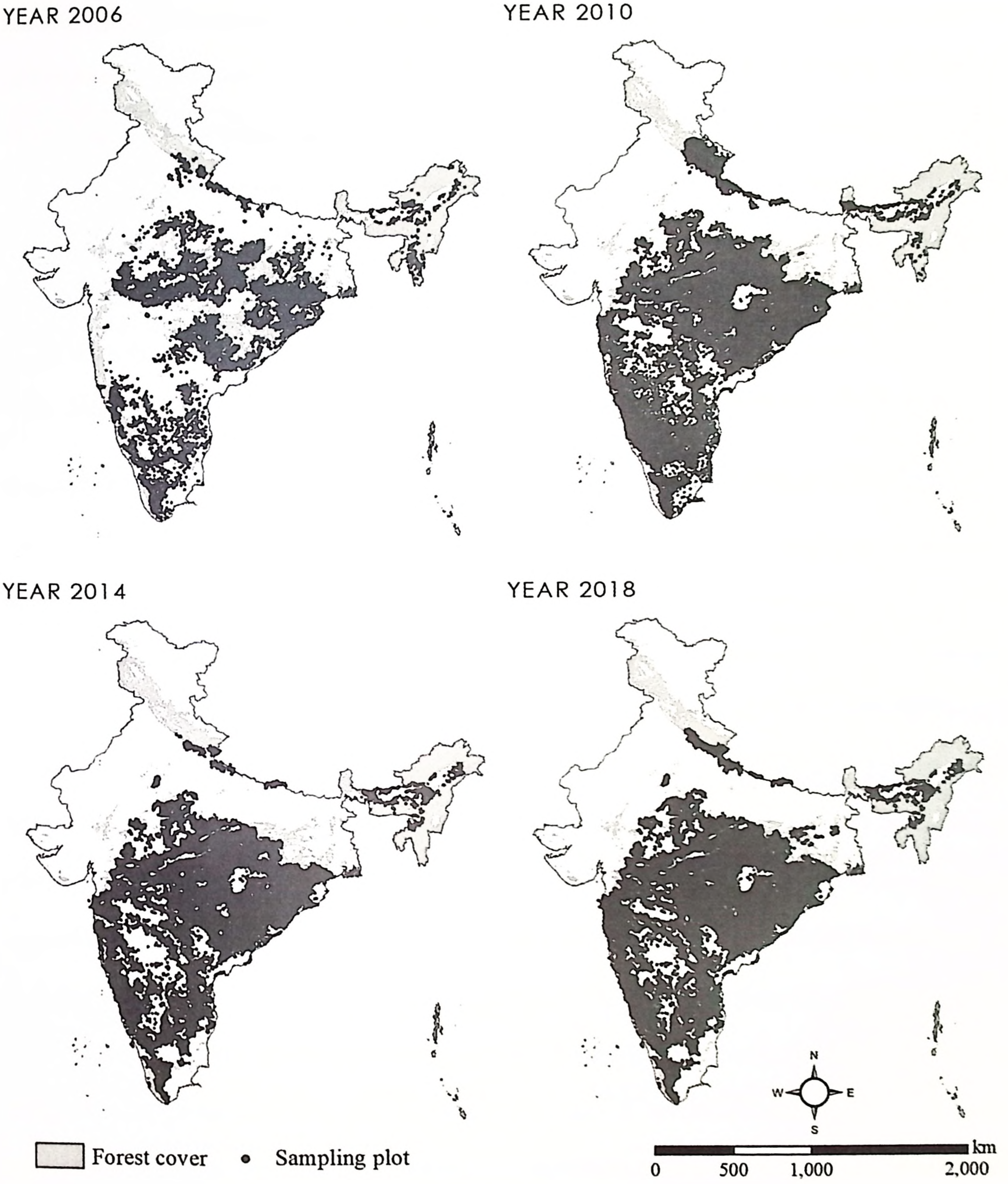

Figure 3 Sampling efforts: Map of sampling plots for invasive plants (30m diameter) across the tropical forests of India during the sampling cycle of the year 2006, 2010, 2014 and 2018

Table 3 Rate of invasion: Change in the area invaded by high concern invasive plants in the common region sampled in the year 2006, 2010, 2014 and 2018.

Species	Area invaded in common grids (km^2)				Rate of change per year (km^2)
	2006	2010	2014	2018	
Ageratina adinophora	22,105	24,590	28,032	31,629	800 (±46)
Ageratum conyzoides	25,211	26,446	31,550	32,084	643 (±152)
Chromolaena odorata	37,934	42,292	51,891	53,911	1438 (±245)
Hyptis suaveolens	9,658	10,584	13,549	15,792	534 (±71)
Lantana camara	70,806	73,221	79,941	82,004	1008 (±159)
Mikania micrantha	32,317	43,547	46,765	49,810	1392 (±352)
Mimosa diplotricha	18,481	19,003	20,464	21,007	226 (±33)
Parthenium hysterophorus	39,565	36,069	35,784	30,971	-652 (±146)
Prosopis juliflora	45,850	49,211	56,034	59,825	1219 (±116)
Senna tora	65,380	67,070	70,111	71,890	564 (±46)
Xanthium strumarium	8,040	8,979	9,564	11,167	249 (±36)

Discussion and organization of thesis

By repeatedly sampling ~26% of the Indian forest in four consecutive cycles across 12 years, present study represents globally unparalleled effort for surveying and monitoring invasive plants. Results suggest that either of the high concern invasive plants have invaded more than 85% of sampled forests at varying densities. In India, where deforestation has occurred at the conservative rate of 173 (±39) km^2/year over last decade (Ravindranath et al. 2012), plant invasion at current rates can only deteriorate the quality of the last remaining forests. This highlights two critical issues; first, the ostensibly consistent increase in forest cover of India is not necessarily indicative of forest conservation or its quality. For an example, the areas reported as increased forest in the state of Rajasthan significantly coincides with areas invaded by a woody shrub *Prosopis juliflora*. Secondly, managing few of these invasive plants involves a cost of ~USD 13,500 /km^2 (Love et al. 2009). With the current distribution extent, managing these species at country-scale can be a costly affair, and requires prioritized approach.

Prioritizing management has an important scientific conundrum of availing timely evidences. Amidst a global decline in fieldwork for conservation (Rios-Saldaña et al. 2018) and the tragedy of conservation in tropical countries (Barlow et al. 2018), mandate for managing invasive plants is usually practiced in isolation with no information on 'where are invasive species spreading?'. As a result, when political ambitions for managing invasive plants are expressed (e.g. India's national report to CBD), the response is either delayed or left to expert opinions (Mathur et al. 2015). This delay in knowing the necessary scientific information for doing timely management can manifest in the "knowing-doing gap" and mutual blaming, which is observed in scientists and managers engaged in invasive species management globally (Matzek et al. 2014). Findings of current monitoring program can be used to identify and prioritize management inside as well as outside protected areas. More importantly, present monitoring protocol is not only suggestive in nature, but also proactive, where the sampling team is equally involved in management at different administrative scales. In addition to evidence-based science, present sampling protocol convinced stakeholders to monitor invasive plants for conserving the forest habitat, which in turn will help build the herbivore densities, and in turn will ensure sustenance of top predators, including the tiger. Importance of managing a multi-trophic ecosystem, which was classically encouraged by many conservationists (Weber & Rabinowitz 1996; Ripple & Beschta 2012; Jhala et al. 2015; Barlow et al. 2018), was thus conveyed in practice.

There might be inherent limitations while using the present scale (i.e. 25 km^2) for comparison, as the changes in densities at sampling scale (~700 m^2) may be neutralized or stay undetected. However, as the densities are recorded at multiple micro-scale plots, one could evaluate the optimal scale at which the densities are representative and further calibrate it with the probability of missing a detection (chapters 5 and 6). Moreover, the sampling framework provides a globally quintessential opportunity to compare invasion trend with rate of anthropogenic disturbances, floral assemblage, carnivore and herbivore occupancies, are recorded at the same spatiotemporal scale (Jhala et al. 2008, 2015; Jhala 2011). Few fundamental theories in biogeography and invasion ecology (e.g. niche conservatism, rapid evolution, anthropogenic facilitation) that were challenged due to unavailability of systematic data (Qiao et al. 2017), were tested using present database (e.g. Chapter 4).

Serving as a unique platform to host scientific and management curiosity, the present monitoring protocol is mandated for continual application in India. Replicating present sampling in outside tiger range areas is not only crucial for conserving these ecosystems, but can also strengthen the managers and scientists working on these plural tropical ecosystems. Presently, many Southeastern and South Asian countries use Tiger as a flagship species to garner resources for holistic conservation (Dhakal et al. 2014; Dey et al. 2015). These projects lack the component on habitat assessment and monitoring; but the present framework for habitat assessment has been proposed for implementation across the global tiger range. Thus, similar studies could be replicated in countries seeking cost-effective, holistic, inclusive and timely evidence on changing landscapes to invoke adaptive management.

SAVANNA SYSTEMS

Savanna system in multi-use areas of Waghapur, Pune. This hillock has been only partially invaded or uninvaded by plants like *Prosopis juliflora, Xanthium strumarium, Cassia tora* and *Parthenium hysterophorous*

@Rajat Rastogi

Savanna system in protected area of Ranthambhore Tiger Reserve. This forest system is invaded by plants like *Prosopis juliflora, Xanthium strumarium* and *Cassia tora*.

@Rajat Rastogi

Native dry deciduous forest system in Kanha Tiger Reserve with diverse grassy and herbaceous understorey

@Rajat Rastogi

Invaded dry deciduous forest system in Kanha Tiger Reserve with monotonous understorey of invasive *Lantana camara*

MOIST DECIDUOUS FOREST SYSTEMS


@Rajat Rastogi

Native moist deciduous forest system in Corbett Tiger Reserve with diverse grassy and herbaceous understorey


@Rajat Rastogi

Invaded moist deciduous forest system in Corbett Tiger Reserve with monotonous understorey of invasive *Lantana camara* and *Ageratina adenophoro*

@Rajat Rastogi

Native semi-evergreen forests with diverse trees and shrubs in the Silent valley National Park

@Ashwin Warudkar

Native semi-evergreen forests with monotonous invasive *Ageratina adenophora* in the Nilgiri Bioshphere Reserve

@Rajat Rastogi

Native evergreen forests with diverse trees in the Periyar Tiger Reserve

@Ashwin Warudkar

Native evergreen forests with monotonous invasive *Ageratina adenophora* and *Chromolaena odorata* in the Nilgiri Bioshphere Reserve

@Rajat Rastogi

Native evergreen shola forests with diverse trees and mosaic of wet grasslands in the Nilgiri Bioshphere Reserve

@Ian lockwood

Native evergreen shola forests invaded.by monotonous woody invasive plants like Acacia mearnsii, *Eucalyptus globulus and Pinus patula* in the Nilgiri Bioshphere Reserve

@Ashish Prasad

Native grasslands of Valmiki Tiger Reserve with minimal invasion of *Mikania micrantha, Chromolaena odorata, Lantana camara* and *Mimosa diplotricha*

@Saurabh Verma

Grasslands of Chitwan National Park with monotonous invasion of *Mikania micrantha, Chromolaena odorata, Lantana camara* and *Mimosa diplotricha*

CHAPTER 4: ON THE NICHE PLASTICITY OF INVASIVE SPECIES

Part of the chapter was published as a peer-reviewed publication: Mungi NA, Qureshi Q, Jhala YV. (2020) Expanding niche and degrading forests: Key to the successful global invasion of Lantana camara (sensu lato). Global Ecology and Conservation 23:e01080. https://doi.org/10.1016/j.gecco.2020.e01080

"When a species colonizes an island that happens to be free of its former competitor, evolutionary release can (and often does) occur. There is a tendency for the variances of the ecologically important characters to increase, and for the species to converge in the direction of one or more of the absent competitors"

-R.H. MacArthur and E.O. Wilson, *The theory of island biogeography*, 1967

Introduction

As our planet change at a prodigious rate, species can either evolve physiological tolerance to sustain, or shift to a suitable environment (Araújo & Pearson 2005; Wiens et al. 2010). While most plants are limited by their dispersal ability (Petitpierre et al. 2012), invasive plants are claimed to invade climatically novel areas (Medley 2010; Guisan et al. 2014); a claim that suffers empirical evidences and statistical biases (Qiao et al. 2017; Yates et al. 2018). The hypothesis of species demonstrating niche change offers a unique opportunity to understand, what succeeds species colonization in a new environment (Elton 1958), and to identify mechanisms that enable or restrict invasions (Medley 2010). Niche models are ubiquitously central to test the hypothesis of niche change (or niche conservatism) but are either vulnerable to limited data or poor statistics (Qiao et al. 2017). The hypothesis further suffers theoretically, where few studies identify the ambiguous definition of niche to be questionable, while others identify the ambiguity in defining an evolutionary unit to compare niche (Smith et al. 2018).

Hypothesis of niche change is mostly tested against the null hypothesis of niche conservatism (Peterson et al. 1999) that states species' niche to substantially mark its evolutionary identity; and consequently, for a species to change its niche is more evolutionary (Pearman et al. 2008). That raises a complex task of defining niche (Colwell & Rangel 2009). Nevertheless, species do not select their ranges from across the spectrum of universal geographies and environments; rather, they optimize traits for the environment within their dispersal limits (Soberon & Peterson 2005). Furthermore, within its dispersal limits, species is constrained by additional stressors like resources, competition, predation, etc. (MacArthur et al. 1972); thus, might be availed to only a subset of its potential niche (*viz.* realized niche). For an example (figure 4), in a hypothetical space U in the tropics (so as to maximize the richness in resources), an ancestral species XX (each initial representative of a genus and of a species) might have established and spread across space Ux. Subsequently, in order to maximize the resource utilization and avoid intraspecific competition, it evolved in two different lineages that resulted in two different species XY and XZ that utilizes distinct geographic subsets of Ux *viz.* Uy and Uz respectively. Thus, evolution of these two species was a response to the resource axis of its niche, while retaining most of other traits in its 'extended phenotype' (e.g. both the species had climatic tolerance for Ux, but due to resource variability they occurred only in the climatic subsets of Uy and Uz). Further, one of the species (XY) was introduced to another tropical space U`, which shares resource and climatic similarity to U. Initially, the species would prefer the conducive space similar in resources with its native area (Uy`), but in absence of competition, or is presence of abundant resources across U`, it will occupy the varied resources within its climatic space. However, if the climatic axis of its native niche i.e. f(Uy) is compared with its climatic axis of introduced niche i.e. f(Uy`), one would interpret f(Uy`) > f(Uy) as an evidence of climatic niche expansion. However, the species was equally able to utilize the climatic space in both regions, but constrained in its native region due to competition. The climatic niche conservatism should, thus, be tested within Uy ∪ Uz and Uy`. Thus, species, as an evolutionary unit, is not always fit for testing the hypothesis of niche change (or conservatism); and one might have to go beyond the species units by lumping, splitting or partial pooling of different units (Smith et al. 2018).

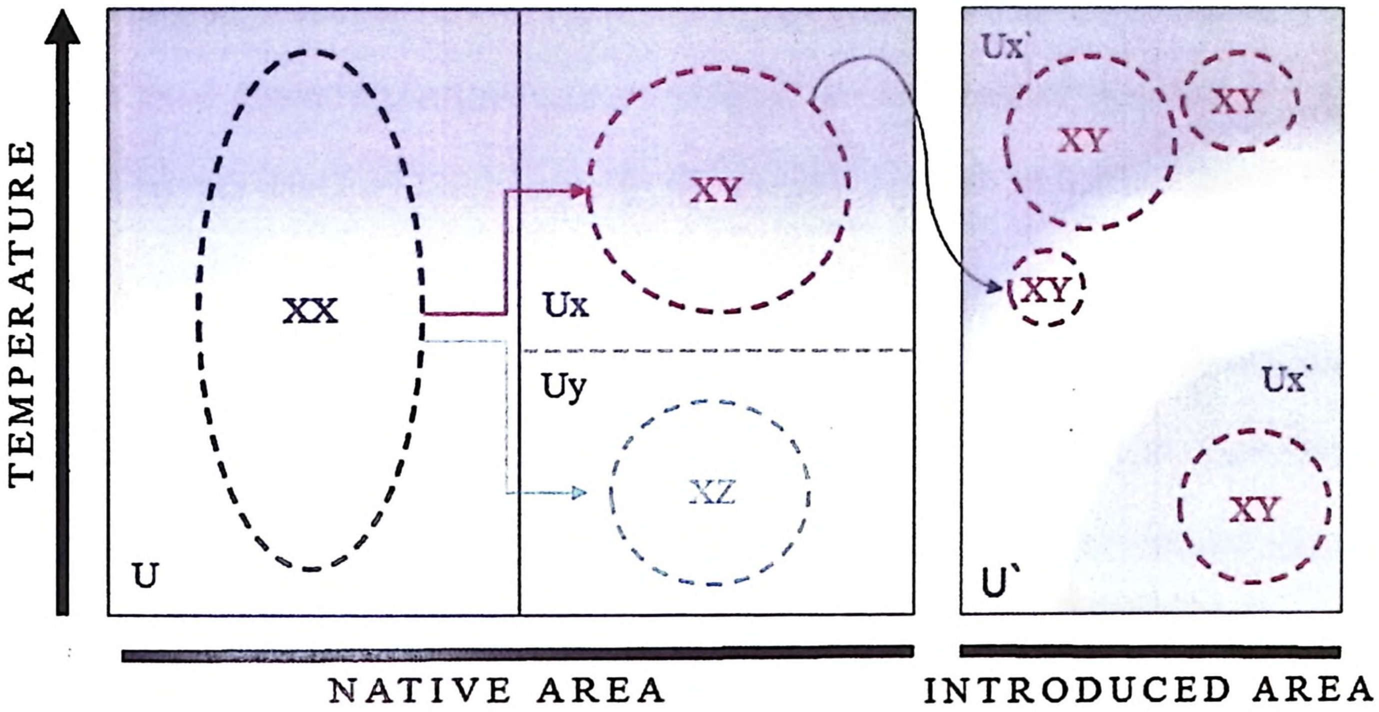

Figure 4 An ancestral species (XX) was spread across the resources gradient (gradient of grey) and temperature available in the native range (U). It speciated on the axis of resources into XY and XZ that utilized subsets of temperature and resources in Ux and Uy respectively. XY was introduced into a novel area (U`) with analogous temperature and resources, where in absence of XZ and rich resources it spread across the temperature (Ux`) that was similar to Ux + Uy. If the temperature axis is compared between Ux and Ux`, expansion is inevitable; in reality Ux` should be compared with Ux + Uy.

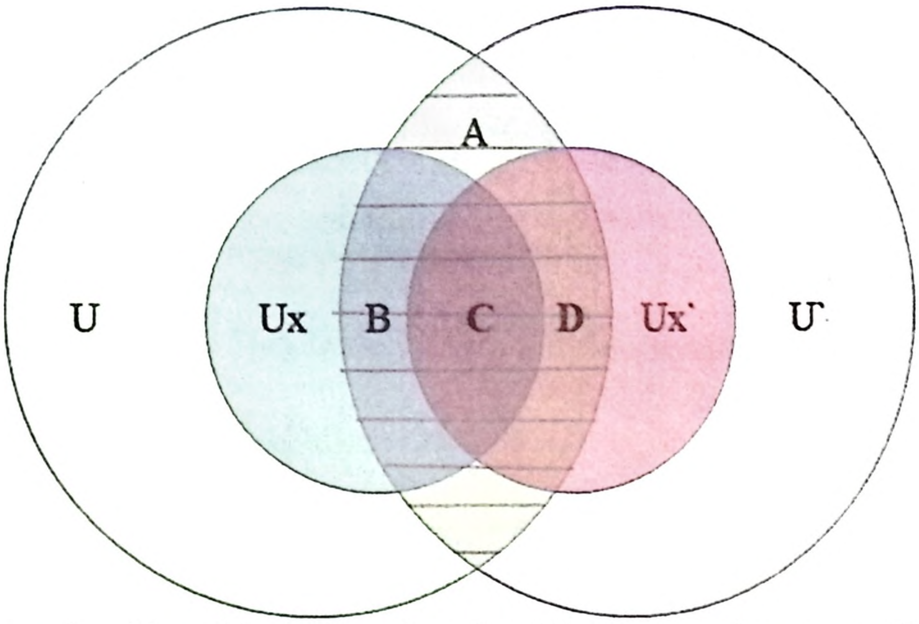

Figure 5 The native region U and introduced region U` shares only an area A, which is analogous ecologically. A species that utilizes a subset (Ux) of U, when introduced in U` utilizes a subset (Ux`). However, the only analogous area where the test of niche change can be done is A, where B represents the niche utilized in native region but not yet utilized in the introduced region, C represents niche retained, and D represents expansion of the niche.

It also highlights the principle problem of identifying key dimensions of the niche on which the assessment of change (or conservatism) should be made, because, "if niche is defined very simply, then niches will be conserved quite commonly" (Peterson 2011). On a contrary, if the niche is defined by many variables so as to address variation at every occurrence and every scale, the niche will always be different in the novel analogous areas. Hence, selecting few dimensions out of the "n-dimensional hypervolume" should be based on the ecological relevance of the predictor dimension (similar to the Liebig's law of the minimum). Ideally such information is should be based on the physiological, behavioral or morphological traits of the species, so as to model its mechanistic niche (Kearney & Porter 2009). But this information is hardly available for species, and hence correlative models that assume the relationship between species occurrence and environmental parameters are more popularly used (Phillips et al. 2006a). Out of many available parameters, usually the ones that parsimoniously and significantly correlate with the species occurrence are used. Although, previous studies have identified limitations of such selection procedure, it remains one of the most popularly published method. Howsoever exclusively used, it is pertinent to select only those predictors that index a mechanism relevant for species occurrence, or atleast for its physiological limits. This approach is a middle path of drawing inference from ecological mechanisms, while still using correlative models.

While the selection of evolutionary unit and ecological axis for niche comparison is based on the ecological criteria, the predictive power of such spatial projection rests on the statistical premise of the model. For a valid comparison, it is essential that models used for explaining niche be within the same ecological space used for training and prediction (Barve et al. 2011). Often this basic assumption of statistical modeling is violated, and inferences are then questionable (Rodda et al. 2011; Qiao et al. 2017). Since, niche change in short spans of time challenge established evolutionary theory of niche conservatism, mere exploratory model-based inferences are often inadequate. Valid niche changes should be assessed only when analogous accessible areas are available to the invasive (region A in figure 5), but the species prefers a new environment in invaded areas as compared to its native range. If the environment in both the areas do not overlap, then niche similarity based of modelling has little value in understanding and interpreting niche change (Peterson 2011). Climatic niche change in analogous areas is often used as a proxy for fundamental niche change, changes estimated from non-analogous areas can be used as a proxy for realized niche change (Webber & Scott 2012; Escobar & Craft 2016). Unlike the climatic niche change, which hints at physiological adaptations in a species, realized niche change provide a unique natural experiment to disentangle the biogeographic responses of the species when freed from natural controlling agents like predators and diseases. Hence, increasing number of studies include influence of biotic parameters in understanding niche changes in invaded area (Tingley et al. 2014). Changes in realized niche also explain how different disturbance regimes and facilitating agents influence the spread of invasive species, thus providing insights for their management. As an example, *Lantana* distribution is known to be influenced by native forest fragmentation in invaded areas (Mungi et al. 2018).

Within the ambit of these three challenges of defining an evolutionary unit, identifying relevant niche axis, and identifying analogous areas to compare the change in niche, present study assesses the potential niche change in 11 invasive plants in India. For this I used primary data from the large-scale monitoring program of invasive plants in India (Chapter 3). This is the largest known systematic monitoring of invasive plants, which is repeated every fourth years, since 2006. It revealed that 90% of the sampled forests are invaded by the high concern invasive plants (Chapter 3). Due to its quintessential spatial coverage across six biogeographic realms, and realistic index of species distribution, it offers a unique opportunity to assess the niche changes in invasive species as compared to their native range. For this, I merge the presence of congeneric species native to the native region of these invasive plants so as to refine the evolutionary unit of comparison. Subsequently, based on the known ecological drivers of these species at various scale (Chapter 5 and 6), I selected niche axes relevant for each species physiology. I used separately the presence of species and covariates from the analogous areas and novel areas of native and invaded region, so as to compare changes in the environmental preference of the species. Our results revealed that few species might have extended tolerance, which is unexpressed in their native region due to competitive segregation from other congeneric species; and expressed only in the introduced areas, thereby realizing the physiological niche. In light of this 'niche plasticity', I discuss its importance in the niche modelling and biogeographic hypothesis testing.

Method

Species occurrence

I selected the presence data of 11 high concern invasive plants (*Ageratina adenophora, Ageratum conyzoides, Chromolaena odorata, Hyptis suaveolens, Lantana camara, Mikania micrantha, Mimosa diplotricha, Parthenium hysterophorus, Prosopis juliflora, Senna tora* and *Xanthium strumarium*) from the three sampling durations (i.e. non-monsoon seasons of 2006, 2010 and 2014). The presence was recorded from the forests of six biogeographic zones present in India (Himalayan foothills and Terrai, Semi - Arid, Central Highlands complex, Deccan, Western Ghats and Northeast), which represents the tropical and sub-tropical climate of the Indian subcontinent that has produced diverse forest types in the region.

I procured spatial presence information of these species and their congeneric relatives from their native range through the Global Biodiversity Information Portal (GBIF). Only those congenerics that are native to the region of the invasive species nativity, were selected. For an example, for invasive *Lantana camara*, I selected the occurrences of the Genus *Lantana* native to the Central and Southern America. For species that had many congeneric species that differed in their habits from tree to herbs, I selected only those congeneric species that are similar to the habit of invasive species. For an example, for invasive *Mimosa diplotricha*, I selected the occurrences of *Mimosa aculeaticarpa, Mimosa andina, Mimosa diplotricha, Mimosa disperma, Mimosa invisa, Mimosa* *loxensis, Mimosa microphylla, Mimosa nothacacia, Mimosa pigra, Mimosa pudica,* and *Mimosa strigillosa.* Out of the total presence records available for each species on the GBIF, I further selected only those for which accurate location (accuracy < 1 km^2) was available, and were recorded after the year 1970, the cutoff date for our climate data. Since I did not sample the native range I was dependent on available data on invasive plants distribution in their native range on GBIF. Since, I had presence of invasive plants in only the forested areas of India I selected only the forested areas of their native region (Global Forest Watch 2016) to compare their niches. This presence information was used for developing niche models. The total number of invasive species, criteria-based locations of each species from native and invasive range and GBIF access information is provided in table 4.

Choosing relevant niche axis

The environmental predictors that influence the occurrence of these invasive plants in India have been earlier explored at different scales (Chapter 6) that confirms to use the scale of 1 km^2 so as to understand the effects of multiple relevant predictors on physiological limits of the species. Details on the relevance of every covariate is provided in chapter 6. These predictors can be classified into three sets of: climate (maximum temperature of the warmest month, mean temperature of the coldest quarter, annual precipitation and precipitation of the driest quarter), resources (soil cation exchange capacity and evapotranspiration), competition (canopy cover). I used species ecology and primary observations (Appendix 3) to select relevant covariates. Other chapters identified anthropogenic modification like nightlights, roads, etc. to influence the spread of these invasive plants (Chapter 5 and 6). I do not consider these parameters as they are not known to influence the physiological limits of the species; and often the relationship with disturbance is dynamic in space and time. For climatic parameters, I used Worldclim (Version 2.0), which provided averaged climate data derived from global and regional weather stations from the years 1970-2000 (Fick & Hijmans 2017). For soil cation exchange capacity, I used the Global

Harmonized Soil data (Nachtergaele et al. 2010). I used Enhanced Vegetation Index (EVI) acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS) from the National Aeronautics and Space Administration (NASA) (Huete et al. 2002) as an index of canopy cover. I assessed the correlation amongst different covariates using Pearson's correlation test (Appendix 2) and used only one covariate in case of higher correlation ($-0.7 > r > 0.7$).

Identifying analogous areas in native and invasive range

To establish a valid comparison between the native and invaded range, I defined the analogous climatic area by considering the following variables: maximum temperature of warmest month, mean temperature of coldest quarter, annual precipitation and precipitation of driest quarter for Central and Southern America and India at 30 Arc-second resolutions (~1 km). Subsequently I extracted principal components (PC's) from these set of variables after checking and correcting for nonlinear relationships. PC's explaining cumulative variation >95 were used for assessing the climatically analogous areas in native and invasive range. I identified analogous climatic space using three different methods; NicheA, Mobility-Oriented Parity (MOP) and Multivariate Environmental Similarity Space (MESS). NicheA generates two convex polyhedrons around the native and invaded climatic space, and estimates the overlap between polyhedrons, which represents similar climatic conditions in both the ranges. This overlapping climatic area of the polyhedrons was projected to the geographic space of both the native and invaded range to identify analogous areas (Escobar & Craft 2016). MOP measures Euclidean distances between climatic space of native and invaded range and excludes that climatic space, which is outside the sampled region (Owens et al. 2013). MESS identifies dissimilar areas based on the statistical distance of climatic variables in native and invaded range from their common mean value (Elith et al. 2011a). While these three methods (NicheA, MESS and MOP) identify multivariate similarity in two areas, there might be a novel climatic combination that is not present in the native area, but present in the invasive range. To address this correlational similarity, I used ExDent tool (Mesgaran et al.

2014) in the areas identified as similar by the former methods. The final area identified as analogous between Central and Southern America and India was the common area derived by intersecting the results obtained by these four models in GIS domain. This final analogous area was used for modeling climatic niche in native and invaded range of Lantana.

Niche modelling

To compare niche between native and invaded range, I used Maximum Entropy (MaxEnt) (Phillips et al. 2006b), one of the most widely used algorithm for niche modeling. MaxEnt calibrates environmental variables from species presence locations and compares them with a set of random sample locations from the study area (Presence-background model). It uses this calibrated relationship of species presence with environment variables to seek similar locations that would likely support the target species. The most unconstrained model developed is considered as the MaxEnt model.

I divided the presence data of each species into training (80%) and testing (20%) sets, using k-fold partitioning design, with k=5. I used each k-partitioned set, for every species, as an input data for MaxEnt.

Statistically, MaxEnt is a presence-background model that compares the presence locations with available environmental space (Phillips & Dudı 2008). The range of background environment substantially influence the response curve and subsequent modeled distribution, which necessitates appropriate ecological criteria and sampling strategy to define the background (Elith et al. 2011b; Webber et al. 2011). The present study had two sets of background environment – native (Central and Southern America) and Invaded (India). Since I only consider forested landscapes, species presence was obtained only from the forested areas of both the regions. Within the forests of India and Central America that had recorded invasive plants presence I randomly selected 10,000 points (no more than one in one km^2) to estimate the background environment. The covariates of climate, resources and forest cover from these background data were used to define the available environment. Species presence points determined the selection of niche space in this environment by the species.

In the present study, linear, quadratic and product features were used to generate the MaxEnt model with 100 replicates for India and Central America each. In order to avoid autocorrelation of the GBIF records, which tends to be biased towards more visited popular areas, I randomly selected only one presence with every pixel area (1 km^2). I did not use any bias correction protocol for India, as the data was systematically collected across the study area. Area Under the receiver operator characteristic Curve (AUC) of MaxEnt model was considered as a criterion to assess the ability of MaxEnt model to predict Lantana presence. MaxEnt produces niche probability for every pixel that varies from 0 to 1. Due to unavailability of true absence data in native region, I could not assess the power of model to classify the absence as true and relied on the threshold provided by maximum sensitivity plus specificity index provided by MaxEnt. I average the results of all the k-partitioned model runs, for each species.

Climatic niche change

I used the analogous areas in native and invasive range to estimate the change in species' realized climatic niche, if any. I define species' realized climatic niche as the set of climate in which the species has evolved its physiological limits (Atwater et al. 2018). I used two sets of occurrence data from the native region: only invasive species, and a group of con-generic species. Climatic variables with presence location in the native range were used in MaxEnt to produce native climatic niche, which was projected to India to derive potential climatic niche of the species. Further, species presence obtained from ground survey in India and same climatic covariates were used to model its climatic niche in India. The difference in potential and observed climatic niche in India was estimated by using Schoener's D and niche similarity test available in 'ecospat' package of R.

Biotic niche change

I used the entire native range (Central and Southern America) and Invasive range (India) to compare the change in response of species to climate, resources and forest cover. For this, I used two sets of occurrence data from native region, similar to the climatic niche analysis; and modeled the biotic niche, using each set, for the native region. I projected this model to the invasive range so as to model the potential biotic niche. Subsequently, I used the species presence and covariates from India to model the observed biotic niche of each species. The difference in potential and observed biotic niche in India was estimated by using Schoener's D and niche similarity test available in 'ecospat' package of R.

Niche overlap

To quantify further niche changes, I used the Centroid, Overlap, Unfilling, Expansion (COUE) framework of Guisan et al. (Guisan et al. 2014) to assess the niche changes as centroid shifts, degree of overlap and amounts of unfilling and expansion. I first conducted two independent principal component analysis (PCA) across the projected and observed niches, using the R package "ecospat". The first PCA was done for the projected and observed niche of invasive species, the second PCA was done for the projected and observed niche of congeneric species. Subsequently, for calculating the niche change metrics (stability, expansion, unfilling) with reduced effects of geographical extent, sampling bias and missing data, I rescaled the first two PCA axes to a grain size of 100 × 100 cells (Broennimann et al. 2011). Species presence was then projected on respective niche surfaces, and the density of occurrence for each grid cell was calculated using kernel smoothing, which allows the density of occurrences to be compared with better representation of the occupied environmental space (Broennimann et al. 2011). This allows us to differentiate between the true niche shifts and the apparent shifts caused by presence of environment that was not available in the native range. The projected and observed niches were overlaid and the niche changes were calculated at the intersection area (Guisan et al. 2014) as follows a) niche expansion: environments that are available in both native and invaded niches, but only occupied in the invaded area b) niche stability: environments that are occupied in both, native and invaded areas (c) niche unfilling: environment similar to the native range, which is not yet invaded in the invaded range.

Result

Out of the 406,375 plots sampled over 10 years (2006-2015) in Indian forests, 303,248 plots were detected with at least one of the invasive plants. The total number of species (and genus) presence from native range of the species selected using the aforementioned criteria are provided in the Table 4. A climatic surface in India, similar to the native range of species was calculated by concatenating the product of four metrics (NicheA, MOP, MESS and ExDent); an example of how analogous surface for *Lantana camara* was developed using NicheA (figure 6) and other methods (figure 7) is provided.

Niche modelling using MaxEnt revealed a consistent AUC ranging from 0.88 to 0.97 for all the species. The relative contribution of different parameters while modeling the climatic and biotic niche of invasive species in their native range and invasive range, as well as the niche of congeneric species in their native range is provided in figure 8 and 9. The distribution of invasive species in their native area and invaded area as well as the distribution of the genus in the native area is plotted against the environmental parameters in figure 12. The climatic niche model for native area and projected to invaded area as well as its observed invaded niche, with respect to invasive and congeneric species was mapped for each species and genus, an example of *Lantana camara* is provided in figure 10. For climatic niche, the change in niche centroid (D), similarity significance of invaded and native range, niche expansion, niche stability and niche unfilling for each species is provided in the table 5.

Table 4 Summary of species and congeners occurrence in their native region: The GBIF records selected using criteria for spatial and temporal accuracy for each invasive species and its considered congeneric species. The criteria were formulated so as to filter the species occurrences for desired resolution (1 km) and period (1970-2018).

		Number of presence on GBIF			
Genus	**DOI**	**Total**	**With coordinates**	**After 1970**	**Positional accuracy**
Ageratina	doi.org/10.15468/dl.mhrmw5	48378	21586	19009	12080
Ageratum	doi.org/10.15468/dl.wpfc2i	26441	11329	8750	3358
Chromolaena	doi.org/10.15468/dl.strrgz	40243	17250	14219	4636
Hyptis	doi.org/10.15468/dl.6vqhaz	40457	15029	9869	9074
Lantana	doi.org/10.15468/dl.t8kvcb	77481	44271	37668	18274
Mikania	doi.org/10.15468/dl.yz55vp	62094	20287	15375	14930
Mimosa	doi.org/10.15468/dl.efzy6g	14142	6214	4644	4114
Parthenium	doi.org/10.15468/dl.uu6a3m	15008	6915	5169	3574
Prosopis	doi.org/10.15468/dl.qdbmd8	26045	12657	10212	3587
Senna	doi.org/10.15468/dl.opomn5	176188	72952	52573	12700
Xanthium	doi.org/10.15468/dl.x8te7j	52285	34314	22918	8918

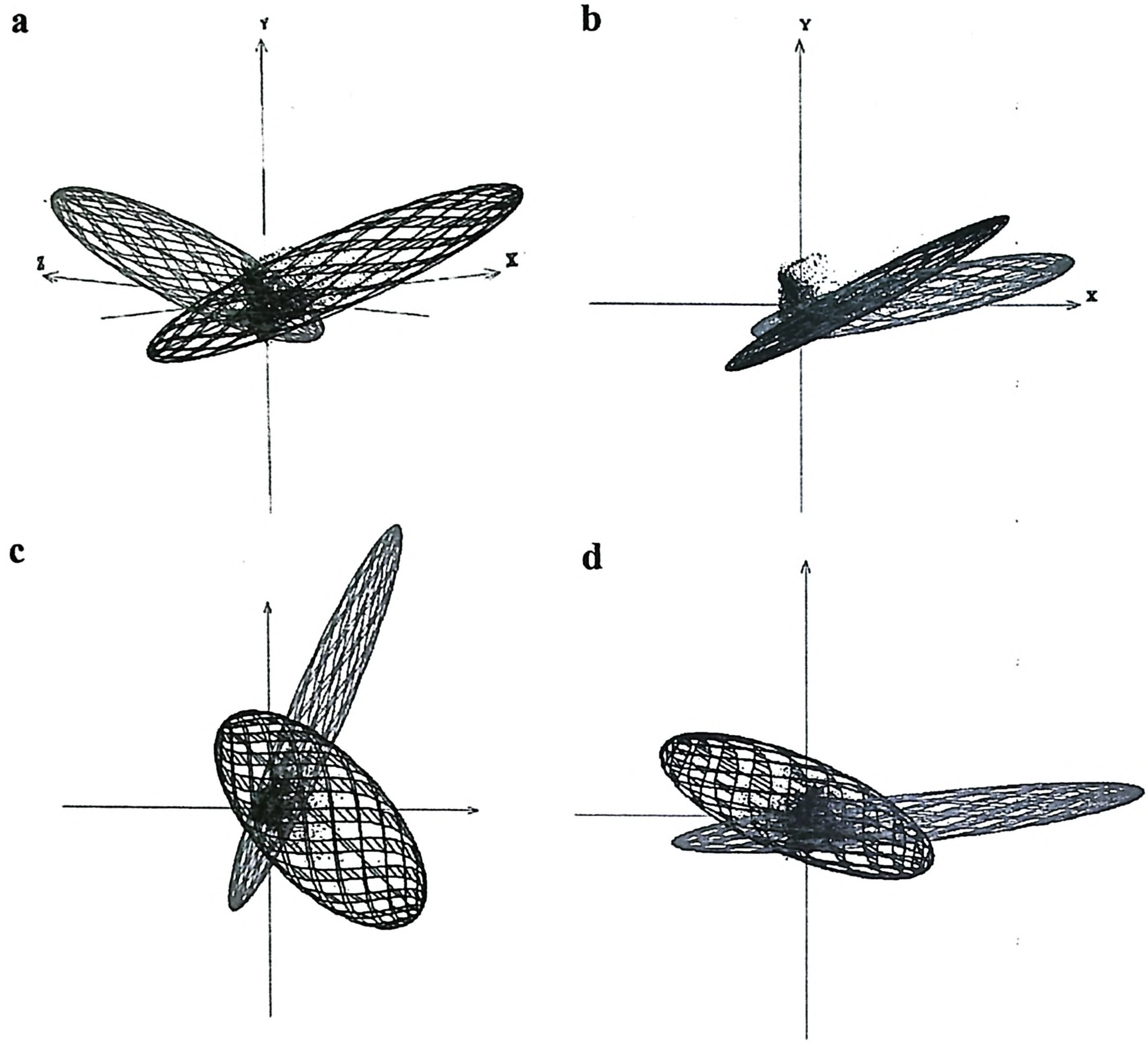

Figure 6 Modelling analogous climate in native and invasive range: Distribution of *Lantana camara* along the three principal components representing climatic factors of native Central America (grey polyhedron) and invaded India (black polyhedron). Black points represent climatic space not occupied by Lantana. Axis X represents increasing annual rainfall and increasing temperature, axis Y represents increasing cooler winters and axis Z represents increasing rainfall. Visualization of distribution on (a) three-dimensional climatic axes, (b) X and Y axis, (c) Y and Z axis, and (d) X and Z axis.

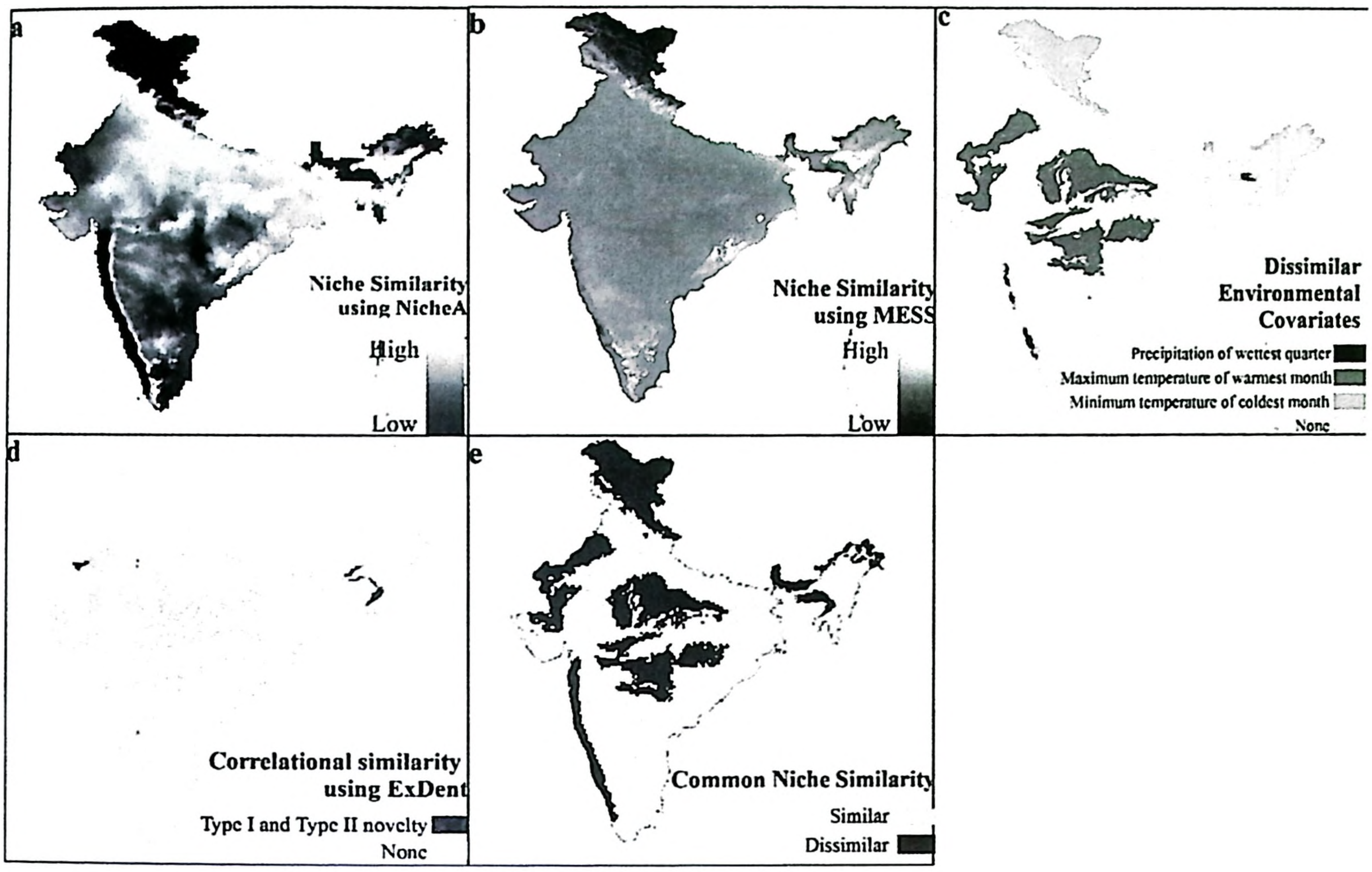

Figure 7 Modelling analogous environments: Map depicting similarity in climate of India as compared to Central America and estimated using NicheA (a), MOP (b) MESS (c) and ExDent (d). The climatically analogous area (e) was extracted by intersection of similar areas identified by all four methods.

While comparing across the entire available analogous environment, the niche centroid (D) was observed to be significantly different in invaded region for all species excluding *Ageratum conyzoides, Prosopis juliflora* and *Xanthium strumarium.* Estimated for niche changes using COUE revealed that for ten out of eleven species (all excluding *Mimosa diplotricha*), species niche in invaded area was significantly expanded. On the other hand, when compared with the projected niche for the respective genus, the expansion was significant for only four species (*Ageratina adenophora, Hyptis suaveolens, Parthenium hysterophorus* and *Xanthium strumarium).* Genus climatic niche was significantly stable in the invaded range, while the species climatic niche demonstrated significant climatic niche expansion.

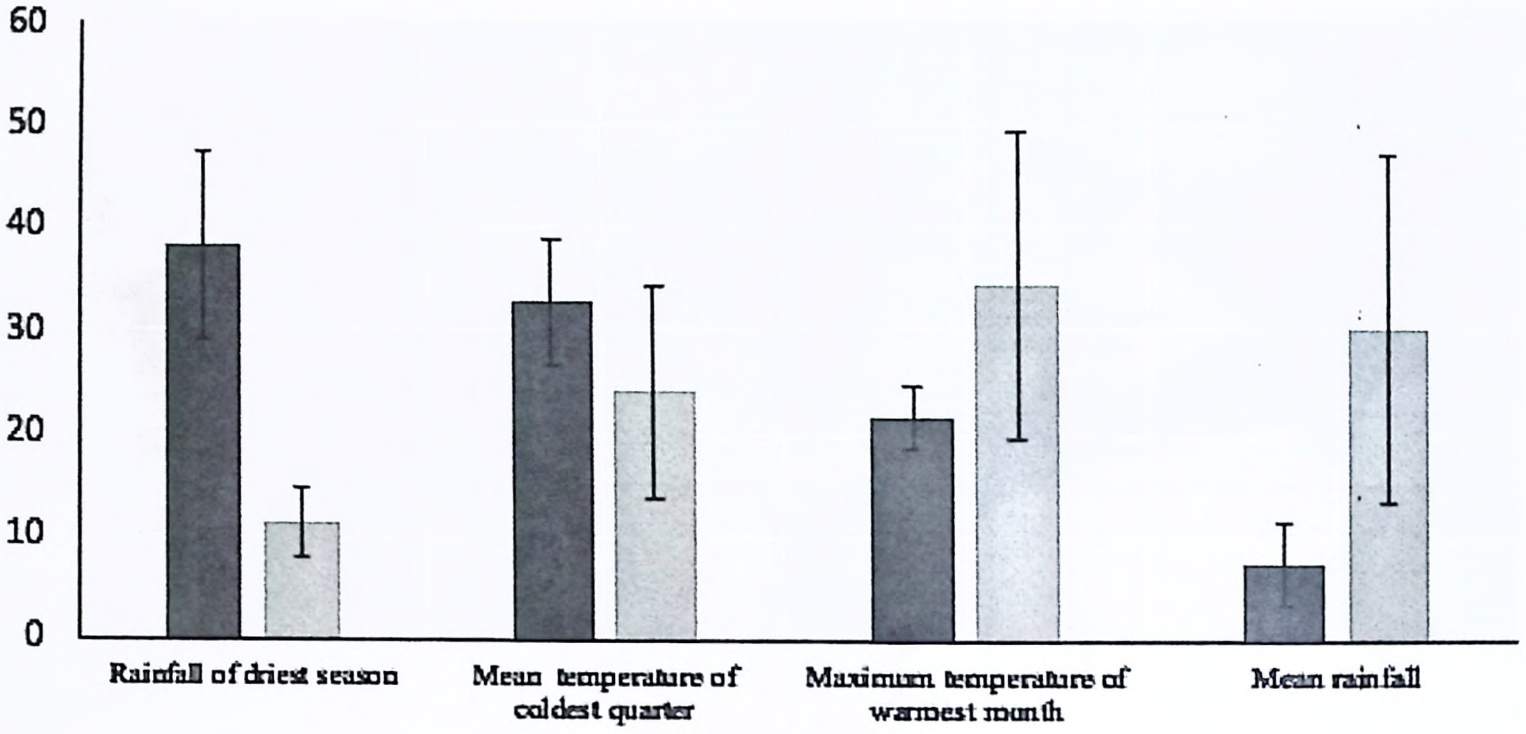

Figure 8 Drivers of climatic niche: Average percent contribution (y-axis) (n=11)of different climatic variables to the climatic niche of invasive plants in its native (light grey) and invaded range (dark grey). Error bars represent standard deviation.

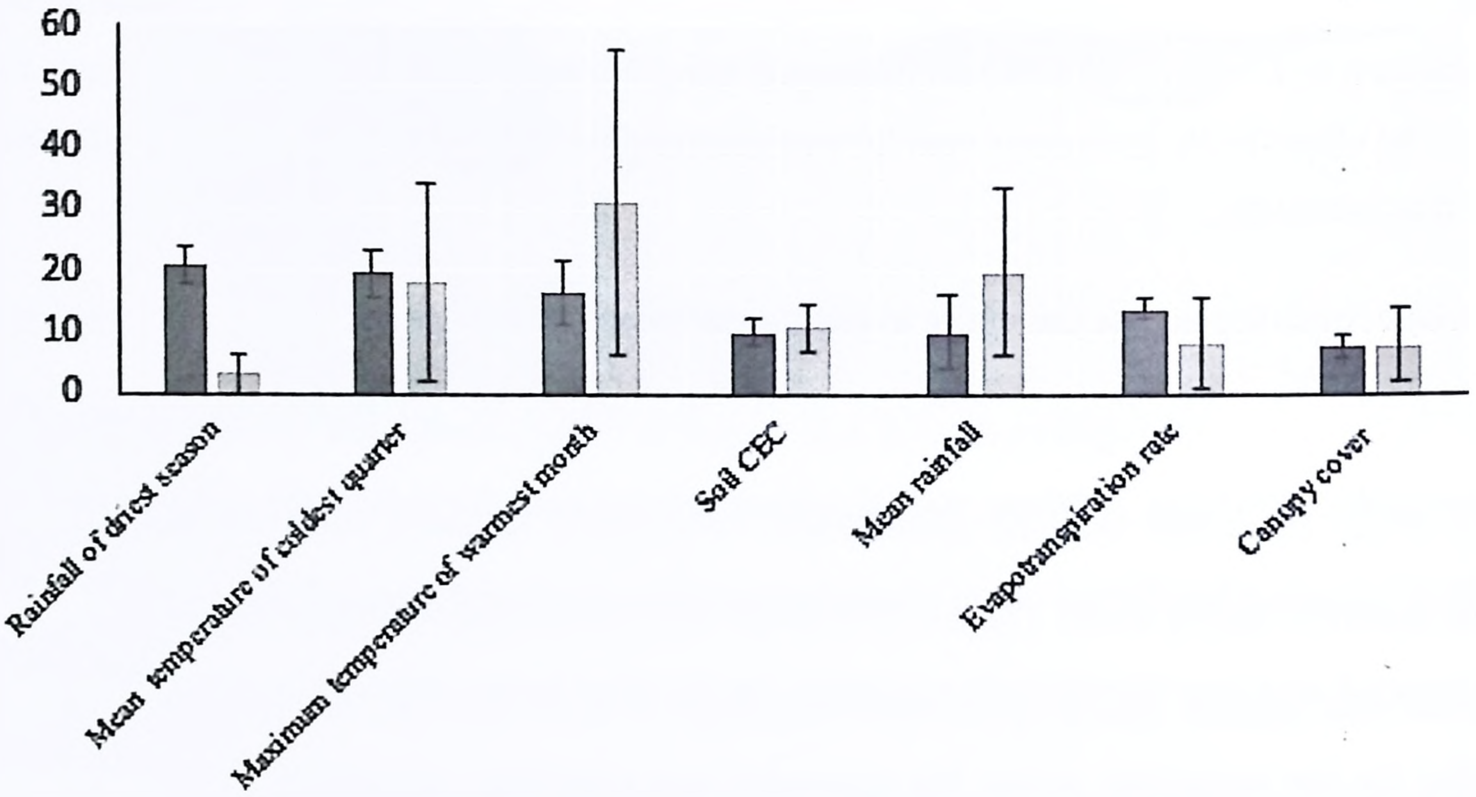

Figure 9 Drivers of biotic niche: Average percent contribution (y-axis) (n=11)of different climatic and biotic variables to the biotic niche of invasive plants in its native (light grey) and invaded range (dark grey). Error bars represent standard deviation.

For biotic niche, the change in niche centroid (D), similarity significance of invaded and native range, niche expansion, niche stability and niche unfilling for each species is provided in the table 6. While comparing across the entire available analogous environment, the niche centroid (D) was observed to be significantly different in invaded region for *Ageratum conyzoides, Hyptis suaveolens Mikania micrantha, Mimosa diplotricha* and *Parthenium hysterophorus.* Estimate for niche changes using COUE revealed that all species niche in invaded area was significantly expanded. On the other hand, when compared with the projected niche for the respective genus, the expansion was significant for all excluding four species (*Mimosa diplotricha, Parthenium hysterophorus* and *Senna tora).* Biotic niche for genus as well as species demonstrated significant expansion. Moreover, all the genus niche and species niche revealed a significant unfilling across the invaded area, in terms of climatic as well as biotic niche.

The response of invasive plants differed substantially in quantities and form between its native and invaded range. While every species response was different, I illustrate the change in the response of *Lantana camara* here (Figure 11). In case of temperature of warmest month, the distribution in India significantly exceeded ($P\text{-value} < 0.005$; Figure 11c) the upper range of distribution in Central America (41° C; Figures 11a and 11b). Lantana showed a parabolic relationship with soil CEC in its native range (Figure 11d) with maxima at 50 meq+/100g, while in India the relationship was a linear decline with CEC (Figure 11e); however, the difference in distribution against soil CEC was insignificant ($P\text{-value} > 0.9$; Figure 11f). In case of pre-monsoon EVI that represents canopy cover, the distribution of Lantana in India was seen to be constrained within a small range which is significantly different subset ($P\text{-value} < 0.1$) of its distributional range in Central America (Figure 11i). However, within this range, the response of Lantana to EVI has changed. Lantana distribution in Central America increased with EVI till the threshold of 0.2 after which it decreased (Figure 11g); while in India the threshold was observed to have shifted to 0.7 and the response was a linear increase with a short asymptote (Figure 11h).

Table 5 Changes in the climatic niche: Indices of climatic niche change for 11 invasive species used in this study. The change in niche centroid (D) and its significance (P) represents change in the centroid of niche hypervolume across analogous areas in native and invaded region. The directionality of this change was estimated using COUE analysis to estimate the change in the projected and observed niches when genus was used (prefix G), and when only species was used (prefix S). the directionality is represented by Expansion (Exp), Stability (Sta) and Unfilling (Unfill), with bold values representing significant changes (>10%)

			G	**G**	**G**	**S**	**S**	**S**
Species	***D***	**P**	**Exp**	**Sta**	**Unfill**	**Exp**	**Sta**	**Unfill**
Ageratina adenophora	0.19	**0.05**	**0.63**	**0.37**	**0.17**	**0.66**	**0.34**	**0.21**
Ageratum conyzoides	0.31	0.18	0.08	**0.92**	**0.74**	**0.19**	**0.81**	**0.65**
Chromolaena odorata	0.43	**0.03**	0.05	**0.95**	**0.14**	**0.38**	**0.62**	**0.17**
Hyptis suaveolens	0.16	**0.03**	**0.7**	**0.3**	**0.61**	**0.43**	**0.57**	**0.68**
Lantana camara	0.56	**0.01**	0.07	**0.93**	**0.17**	**0.16**	**0.84**	**0.25**
Mikania micrantha	0.37	**0.07**	0.08	**0.92**	**0.3**	**0.32**	**0.68**	**0.5**
Mimosa diplotricha	0.58	**0.09**	0.06	**0.94**	**0.79**	0.09	**0.91**	**0.59**
Parthenium hysterophorus	0.57	**0.05**	**0.1**	**0.9**	**0.1**	**0.23**	**0.77**	**0.17**
Prosopis juliflora	0.38	0.26	0.06	**0.94**	**0.2**	**0.19**	**0.81**	**0.16**
Senna tora	0.83	**0.06**	0.07	**0.93**	**0.17**	**0.32**	**0.68**	**0.24**
Xanthium strumarium	0.36	0.18	**0.42**	**0.58**	**0.3**	**0.49**	**0.51**	**0.16**

Table 6 Changes in the biotic niche: Indices of biotic niche change for 11 invasive species used in this study. The change in niche centroid (D) and its significance (P) represents change in the centroid of niche hypervolume across analogous areas in native and invaded region. The directionality of this change was estimated using COUE analysis to estimate the change in the projected and observed niches when genus was used (prefix G), and when only species was used

(prefix S). the directionality is represented by Expansion (Exp), Stability (Sta) and Unfilling (Unfill), with bold values representing significant changes (>10%)

Species	***D***	**N to I (p)**	**G Exp**	**G Sta**	**G Unfill**	**S Exp**	**S Sta**	**S Unfill**
Ageratina adenophora	0.13	0.3	**0.65**	**0.35**	**0.38**	**0.74**	**0.26**	**0.17**
Ageratum conyzoides	0.1	**0.07**	**0.57**	**0.43**	**0.24**	**0.62**	**0.38**	**0.16**
Chromolaena odorata	0.41	0.13	**0.29**	**0.71**	**0.28**	**0.45**	**0.55**	**0.34**
Hyptis suaveolens	0.79	**0.02**	**0.72**	**0.28**	**0.57**	**0.8**	**0.2**	**0.62**
Lantana camara	0.66	0.15	**0.19**	**0.81**	**0.6**	**0.24**	**0.76**	**0.78**
Mikania micrantha	0.12	**0.05**	**0.38**	**0.62**	**0.35**	**0.46**	**0.54**	**0.55**
Mimosa diplotricha	0.63	**0.1**	0.09	**0.91**	**0.52**	**0.15**	**0.85**	**0.47**
Parthenium hysterophorus	0.59	**0.07**	0.09	**0.91**	**0.19**	**0.3**	**0.7**	**0.25**
Prosopis juliflora	0.42	0.33	**0.22**	**0.78**	**0.19**	**0.34**	**0.66**	**0.11**
Senna tora	0.7	0.76	0.08	**0.92**	**0.35**	**0.13**	**0.87**	**0.54**
Xanthium strumarium	0.42	0.3	**0.48**	**0.52**	**0.41**	**0.59**	**0.41**	**0.21**

Similar to *Lantana camara*, a significantly increased tolerance (P-value < 0.05) towards higher temperature, lower soil fertility, denser canopies and higher evapotranspiration rate was observed for *Ageratina adenophora, Ageratum conyzoides* and *Chromolaena odorata.* Another set of species - *Prosopis juliflora, Xanthium strumarium, Hyptis suaveolens* had significantly increased tolerance (P-value < 0.05) to higher rain in driest season, higher soil fertility and lower evapotranspiration.

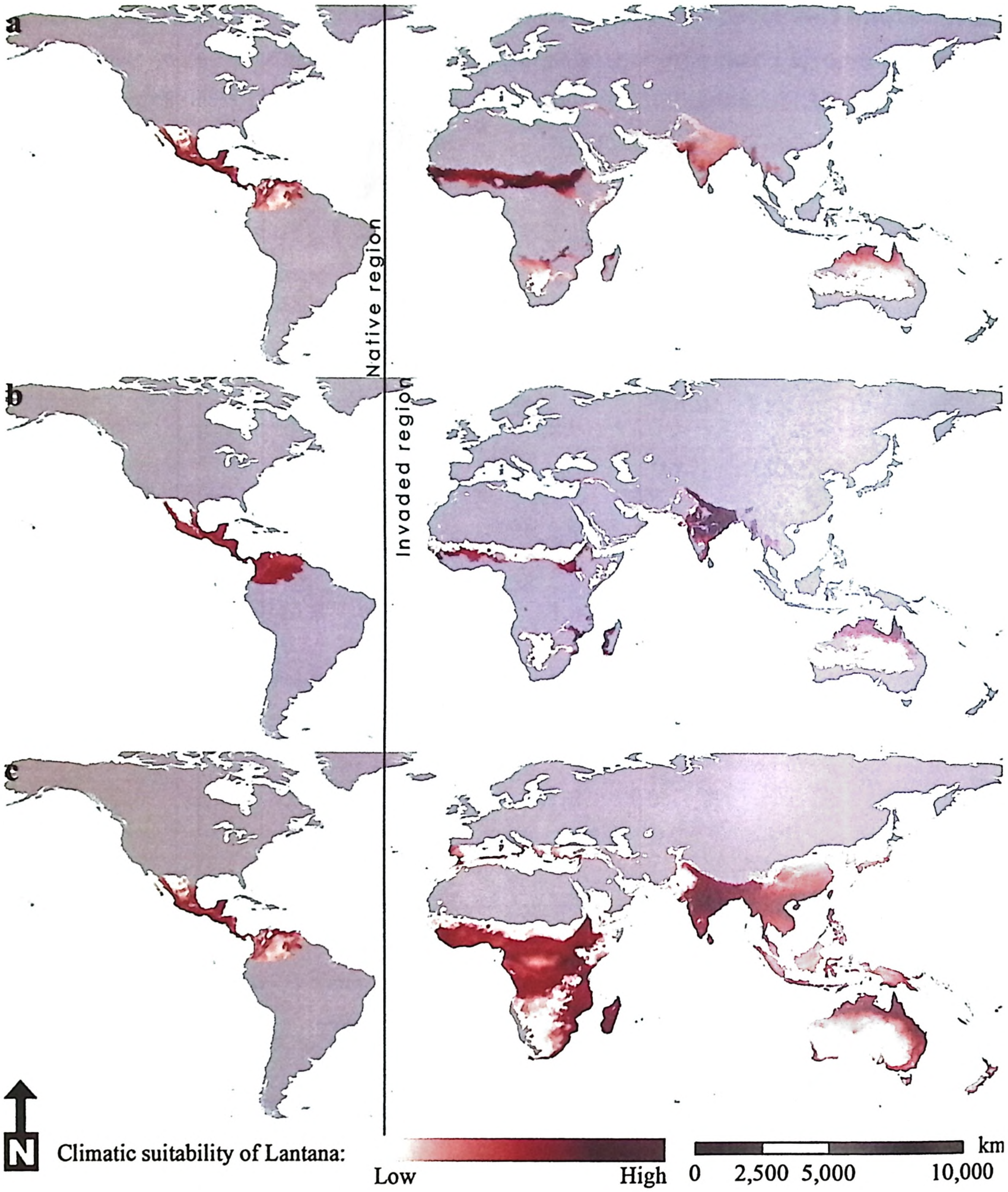

Figure 10 Niche change of *Lantana camara*. climatic niche of *Lantana camara* in its global range: (a) climatic niche of Lantana modeled from presence in the its native range and projected to analogous areas in its global invaded range (b) climatic niche of Lantana in analogous areas of its global invaded range as modeled from its presence in these areas (c) global climatic suitability of Lantana modeled from its global presence.

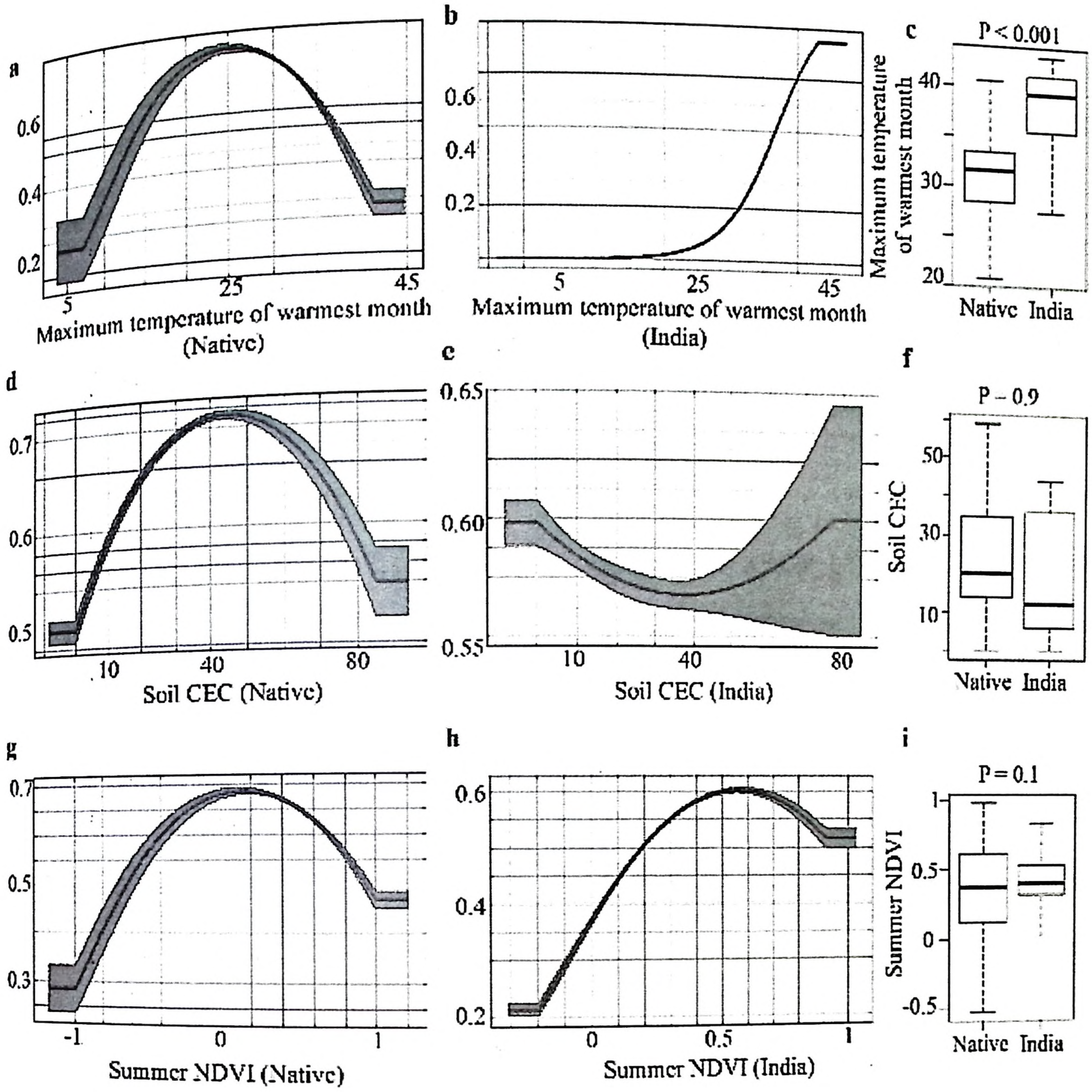

Figure 11 Differential response of *Lantana camara*: Response and distribution of *Lantana camara* in native Central America and in invaded India. Lantana distribution significantly shifted (c) to areas with higher temperature of warmest month in India (b) as compared to native America (a); the response to soil Cation Exchange Capacity (CEC) changed between native America (d) that observed in India (e) but within the same range of values (f); With regard to summer Enhanced Vegetation Index (EVI) the niche width of Lantana in India was a subset of that observed in native America (i), whereas the response was similar in shape in native (g) and invaded range (h) but with a shift towards denser canopy in India.

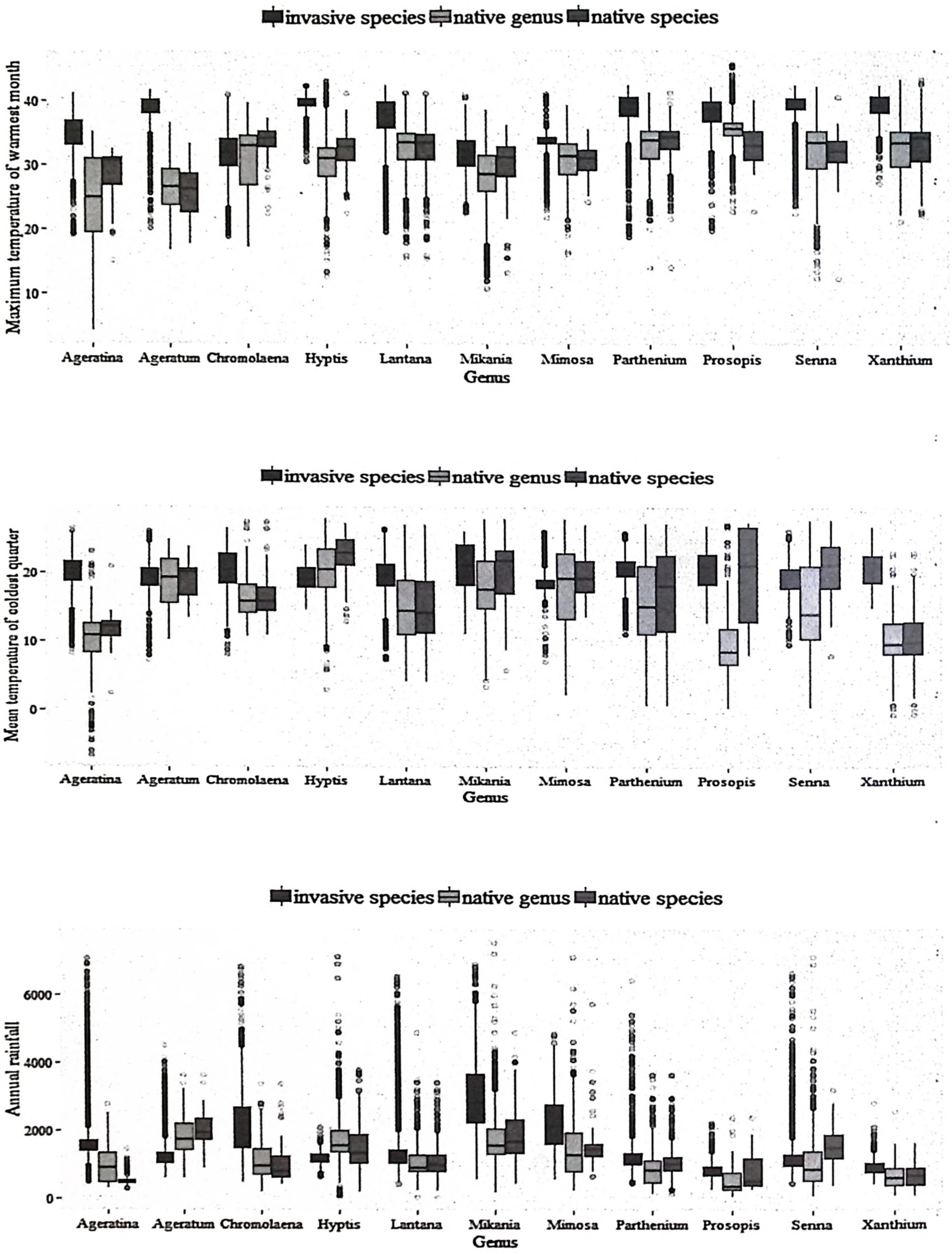

Figure 12 differential response of invasive plants: The distribution of invasive species in invaded area (dark grey) and native area (grey), and its congeneric species in native area (light grey) against the environmental parameters (summer temperature, winter temperature and annual rainfall) considered for modelling its niche.

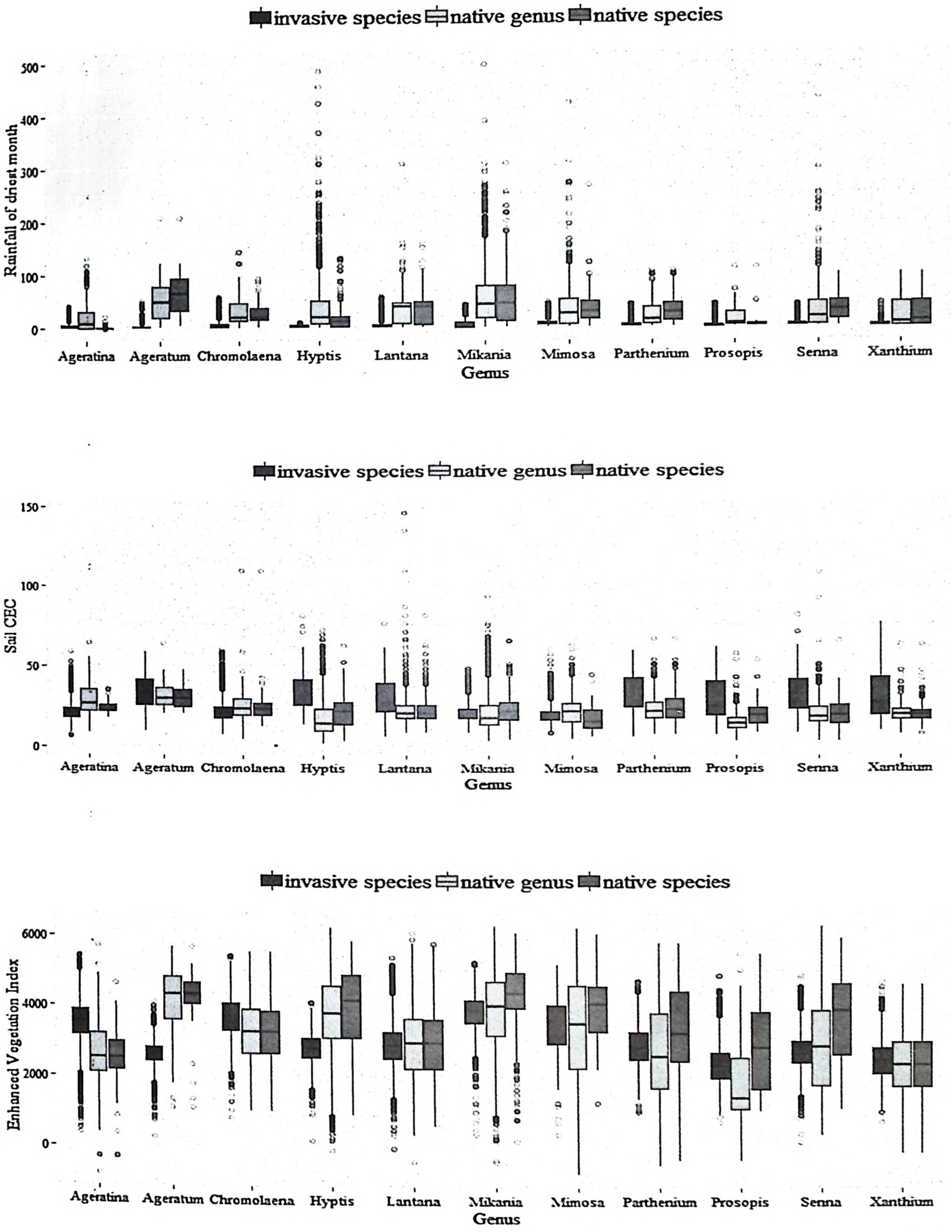

Figure 13 differential response of invasive plants: The distribution of invasive species in invaded area (dark grey) and native area (grey), and its congeneric species in native area (light grey) against the environmental parameters (rainfall of the driest season, soil CEC, enhanced vegetation index) considered for modelling its niche.

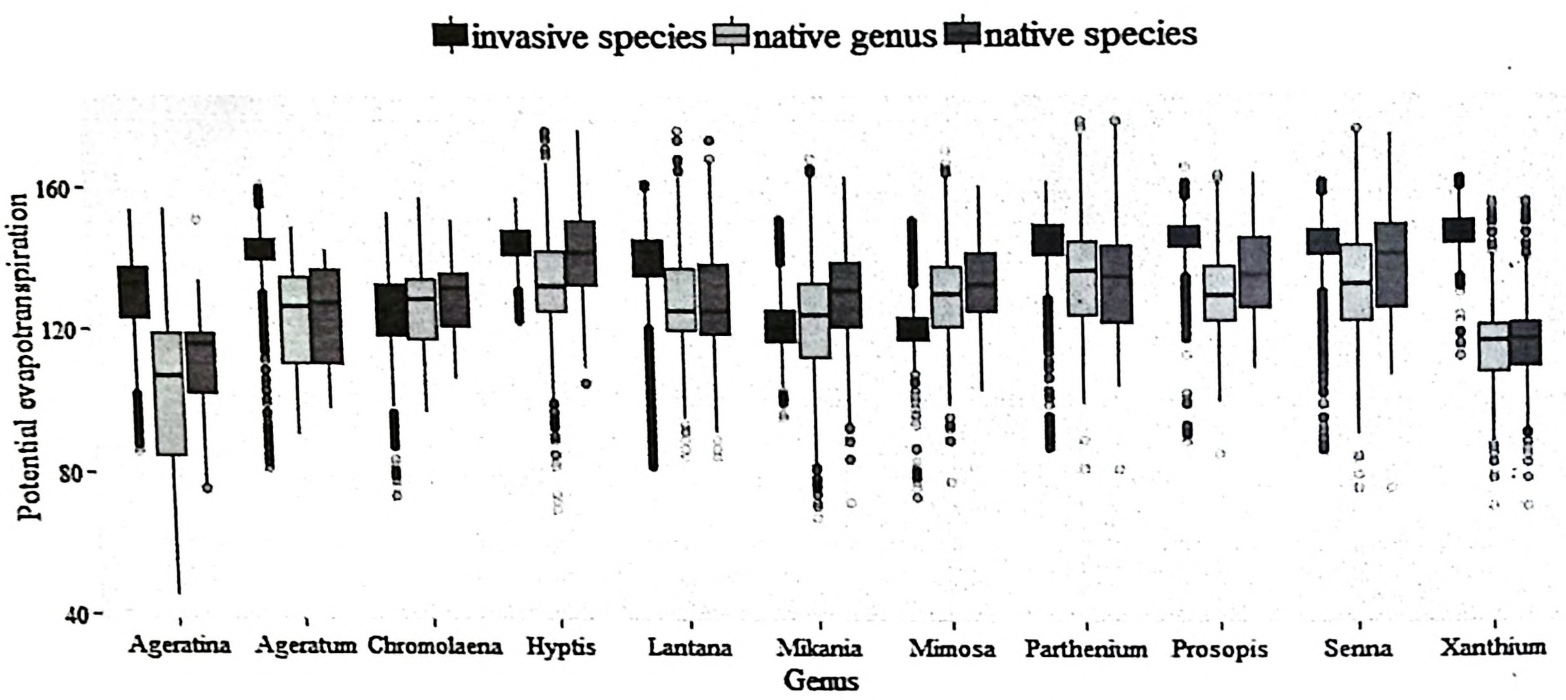

Figure 14 differential response of invasive plants: The distribution of invasive species in invaded area (dark grey) and native area (grey), and its congeneric species in native area (light grey) against the environmental parameters (potential evapotranspiration) considered for modelling its niche.

Discussion

Climatic niche is used as proxy for fundamental niche, which is bounded by the environmental tolerances of the species. Hence, shifts in the climatic niche of species have been proposed as indirect evidence for adaptation by invasive species to novel environments (Gallagher et al. 2010). In the present case study, climate in parts of India was analogous to that observed in Central and Southern America, the native range of invasive plants. Within this analogous climatic space, *Ageratina, Hyptis, Parthenium* and *Xanthium* expanded their climatic niche in India. This expansion in climatic tolerances could be due to either predator/pathogen/competition release or phenotypic plasticity or adaptive evolution in India. Considering the covariates representing climate, soil resources, evapotranspiration and competition by dense canopies (analogous as well as novel) I found that all the species excluding *Mimosa, Parthenium* and *Senna,* had invaded an additional novel niche space on the axis of increasing temperature, lower soil fertility and higher evapotranspiration.

Previous studies (Blossey & Notzold 1995) suggested that escape from specialist natural enemies could result in increased competitiveness of invasive plants leading to contemporary evolution. Owing to the global climate change, many areas are experiencing warmer summers (Sharmila et al. 2015) and increased soil acidity that results in low fertility. Hence, for any invasive plant an ideal phenotypic optimum will be to exploit these changes, which was observed in the case of considered invasion in India. If the species shows significant difference in traits between native and invasive areas it clearly indicates its phenotypic plasticity, which, if responsible for higher fitness of the species, could be considered adaptive (Sultan 1987; Pigliucci & others 2001). This adaptation could be due to unexpressed inherent plasticity or increased plasticity. As the results suggest, invasive plants expressed their potential to exploit the ancestral environment used by its congeneric species in its native region. In the lights of an extended phenotype in most of the tropical organisms, I interpret this phenomenon as Niche plasticity.

I define niche plasticity, as the ability of species to express its extended environmental tolerance in absence of its congeneric competitor, due to which the species had limited to exploit only a subset of its potential niche. Our approach, in concordance with the classical theory of niche conservatism, shows that the niche is not essentially conserved in the species and one has to identify the evolutionary unit, which could conserve the niche axes considered. This could also be substantiated by a new phenotypic expression observed in these invasive species. For an example, the invaded population of Lantana was found to be more tolerant to denser canopies, which could possibly be due to its enhanced competitiveness. A phenotypic variant of lantana in India, which is a climber, enables it to access sunlight even in dense canopied forests. Such phenotypes are not reported from native Central America. A recent study further demonstrated that such phenotypic variation increases the performance and success of Lantana invasion in the forested areas (Goyal & Sharma 2019).

Interestingly, all the species that displayed an expansion in species niche, so as to occupy the genus niche had an explicit history of hybridization after introduction to Indian subcontinent. This may have availed the species to exploit the additional space available in each of the species in its genus. For an example, Genetic studies of *Lantana* in India (Ray & Quader 2014) have found higher genetic diversity and multiple genetic clusters across India, suggesting multiple introductions of *Lantana* with novel founders each time. This was further validated by naturalist record from 19th century that indicated multiple introductions from various sources in India (Kannan et al. 2013b). Another study (Ray and Ray 2014) on *Lantana* in India predicted that the multiple genetic clusters could be responsible for local adaptation and it could represent early stages of ecological divergence. Thus, in addition to climatic niche shift and shifts in response norms, both of which are suggested to be the evidence for rapid adaptation (Gallagher et al. 2010), genetic evidence suggests adaptive changes in the genes as mechanisms explaining the success of Lantana invasion. The above evidences support the hypothesis (De Jong 2005) that phenotypic plasticity provides rapid opportunity for natural selection to operate and facilitates first steps in the adaptive walk by a species, which otherwise would depend on new mutations (West-Eberhard 2003). Nevertheless, further experiments comparing populations from native and invasive areas are required for confirming that these phenotypic changes have a genetic basis to show conclusive support of contemporary evolution.

Previous studies investigating the effects of climatic changes on invasion by invasive species assumed that species-climate relation would be preserved across space and time (Kannan et al. 2013b; Goncalves et al. 2014). Our study results flag a caution on such an approach, which assumes that the niche of a species to be at equilibrium and retain its response to climate. Such assumptions could underestimate the actual threat potential of invasive species to ecosystems.

Diverse habits and habitats of *Lantana camara* in India: Lantana was recorded in different habits across different biogeographic realms in India. Here we show the climber ecotype of Lantana in evergreen forests of the Western Ghats (A); shrub ecotype in the Western Himalaya (B) and dry savannas of Central India (C); Tree (bole girth > 15 cm) ecotype in the mesic savannas of central Indian highlands (D); short shrub ecotype on the coastal sand dunes (E); and emergent shrub ecotype in the wetlands of semi-arid India (F).

CHAPTER 5: MULTI-SCALE DRIVERS OF INVASIVE PLANTS

"The real environment ...is like a checkerboard of habitats, each square of which has, on closer examination, its own checkerboard structure of component subhabitats. And even the tiny squares of these components are revealed as themselves checkerboard, and so on"

- R.H. MacArthur, *Geographical Ecology*, 1972

Introduction

Understanding 'why a species is present at a particular site?' is fundamental to ecology, as it adds to our understanding on how the nested landscape characteristics have contributed in evolution of a species and patterns of biodiversity (Krebs & Krebs 1994). Modelling species distribution with respect to the rapidly changing world has revealed the inability of species to cope with these changes and sustain in future; it has helped in devising policies pertinent to control drivers of such unsustainable changes (McGeoch et al. 2010). While most of these global changes have reduced native species, invasive species, on the contrary, have been facilitated by it (Hulme 2009). Hence, there's a recent surge in understanding how the changing earth system is driving the distribution of invasive species. It is also increasingly addressed that these drivers operate and influence the species at different spatial scales. For an example, a species might be influenced by climate at macro-scale, while at micro-scale, its presence in determined by habitat characters like the availability of resources (McGill 2010). Thus, identifying multi-scale drivers of invasive species is urgently needed to control them at an optimal scale so as to arrest the spread of invasive species.

Species Distribution Models (SDMs) are popularly and successfully used for developing the distribution of various invasive species, globally (Araújo & Peterson 2012). Due to inherent complexities in the data, covariates, scales and processes, SDMs have been consistently subjective in unifying the theories and methods to address multi-scale response of species to the environmental predictors (Fournier et al. 2017). This has resulted in erroneous projection of invasive species in novel area (Qiao et al. 2017) and in the future scenarios (Seo et al. 2008).

Recent studies demonstrated the effect of changes in the spatial scale of predictors (i.e. grain size) on the resultant distribution, suggesting that the choice of scale is important while selecting a predictor based on ecological criteria (Lauzeral et al. 2013). However, these studies, though suggestive of important phenomena, are limited because few of them use only the climatic and other macro-scale predictors (Manzoor et al. 2018); while others have used diverse predictors, but on virtual species (Connor et al. 2018). One of the primary challenges in addressing the lacuna in understanding the effect of different grain sizes on the species distribution is the lack of systematic species occurrence data across large-scale bio-geographic realms. As a result, most of the models adhere to virtual species or large set of data produced from opportunistic sightings (e.g. Ebird, GBIF); and thus have a limited role in advancing theoretical ecology, as well as devising conservation actions.

One such large-scale monitoring program that can help elucidate the multiscale responses of invasive species to important landscape characters is the one conducted in India (Chapter 3). This is the largest known monitoring of invasive plants, which is repeated every fourth year, since 2006. It revealed that 90% of the sampled forests are invaded by the high concern invasive plants (Chapter 3). Due to its quintessential spatial coverage across six biogeographic realms, and realistic index of species distribution, it offers a unique opportunity to test the effects of multi-scale predictors in modelling the distribution of invasive species. Chapter 6 identified the rate at which these species were invading the sampled area; and environmental parameters that facilitated as well as resisted its spread. However, the distribution was estimated for only the sampled areas and at an ecological scale of 25 km^2. These studies suggested a possibility that different environmental predictors influence these species differently at different scale. There is also a scope to use the same data to model the country-wide distribution of these invasive plants using multi-scale SDM.

In the present study, I used MaxEnt to model the distribution of all 11 high concern invasive plants identified in India, at seven different grain sizes (i.e. 250 m, 500 m, 1 km, 2 km, 5 km, 10 km and 20 km). I use a subset of the real distribution of these invasive plants to model their distribution with respect to climate, resources, forest cover, fragmentation and anthropogenic pressures. I presumed that covariates like climate that spatially vary at a large scale will have effect at larger grain sizes (e.g. 5 km); whereas covariates like forest characters and fragmentation that spatially vary at smaller scale (e.g. 250 m) will influxes only at these grain sizes. Subsequently, I assess the effect of different scales on the distribution estimate of each species, contribution of the environmental predictors and model performance. It will not only produce precise maps at country-scale but also help the managers prioritize the actions on drivers that are facilitating the spread of these species, and make evidence-based policies for country-wide management of invasive plants.

Material and methods

I selected the presence data of 11 high concern invasive plants (*Ageratina adenophora, Ageratum conyzoides, Chromolaena odorata, Hyptis suaveolens, Lantana camara, Mikania micrantha, Mimosa diplotricha, Parthenium hysterophorus, Prosopis juliflora, Senna tora* and *Xanthium strumarium*) from all the sampling durations (i.e. non-monsoon seasons of 2006, 2010 and 2014), from the ground sampling plots of 30 m diameter, as mentioned in Chapter 3. The presence was recorded from the forests of six biogeographic zones present in India (Himalayan foothills and Terai, Semi - Arid, Central Highlands complex, Deccan, Western Ghats and Northeast), which represents the tropical and sub-tropical climate of the Indian subcontinent that has produced diverse forest types in the region. These forests are surrounded by one of the densest developing human populations in the world, which is rapidly modifying these forests due to livelihood dependencies and developmental activities like construction of dams, linear infrastructure, mining, etc. Hence, there are multiple drivers, which operate at varying scale to influence the ecological integrity of the forests, which in turn facilitate or resist the invasive plants.

These drivers were identified at 1 km scale for the 11 invasive species and are provided in chapter 6. These predictors can be classified as climate (maximum and minimum temperature, annual precipitation and precipitation of the driest quarter), resources (water availability), forest cover (canopy cover and deciduousness of the forest), forest fragmentation (fire, forest loss and index of forest browning) and anthropogenic pressure (night-time lights and distance from human infrastructure). Not all the predictors were used for all the species, and the number of predictor was based on ecological hypothesis that determined the effect and its contribution to the invasive species distribution. Hence, in place of relying on the parsimonious selection of the predictors to make simplistic models, I choose to develop ecologically informed models (Coelho et al. 2019). I used species ecology and primary observations (Appendix 3) to select relevant covariates. While I use most of the predictors from the same sources, their processing and scaling at different grain sizes used in the study (i.e. 250 m, 500 m, 1 km, 2 km, 5 km, 10 km and 20 km) is elaborated here.

Effect of climatic drivers

Climate data (maximum and minimum temperature, annual precipitation and precipitation of the driest quarter) representing the temperature and precipitation parameters was obtained from Worldclim (Version 2.0), which provided averaged climate data derived from global and regional weather stations from the years 1970-2000 (Fick & Hijmans 2017). It is downscaled by using geographic and elevation information at 1 km resolution. I further downscaled the Worldclim variables to 250 m and 500 m spatial resolution using the PRISM approach (Daly et al. 1997) that utilizes elevation and location information. A 90 m digital elevation model (DEM), obtained from the Shuttle Radar Topography Mission (SRTM), was resampled to 250 m, 500 m and 1 km to provide the required elevation data at the same resolution as the climatic data. Comparing climate to elevation at 1 km, using multivariate regression revealed more than 95% variation in climate explained by elevation, latitude and longitude. The regression coefficients and intercepts were used to derive the climatic variables when the elevation, latitude and longitude were at 250 m and 500 m scale. Subsequently, to derive the climate at larger grain size, the original climate data (1 km) was upscaled at 2 km, 5 km, 10 km and 20 km.

Effect of resources

I used the surface water mapped at 30 m scale, developed by the European Commission's Joint Research Centre (Pekel et al. 2016). I calculated the Euclidean distance from these water pixels at different grain sizes.

Effect of forest cover

I used Enhanced Vegetation Index (EVI) acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS) from the National Aeronautics and Space Administration (NASA) (Huete et al. 2002) as an index of canopy cover. MODIS EVI data has been calibrated to reduce atmospheric and soil background contamination, while significantly correlating with chlorophyll content. I averaged MODIS EVI procured at 16 days' interval at 250 m for the sampling years (2006-2018) to index an average canopy cover. It was further upscaled to different grain sizes.

Subsequently, I averaged the same product, at original scale (250 m), for the pre-monsoon (March, April and May) and post-monsoon (October, November and December) seasons; and the difference was used as an index for deciduousness of the forests. This was further upscaled to other grain sizes.

Effect of forest fragmentation

I obtained information on fire occurrence from the Fire Information for Resource Management System (FIRMS) database, which consisted of daily MODIS hotspots (Giglio et al. 2003) and Visible Infrared Imaging Radiometer Suite (VIIRS) (Schroeder et al. 2014). In total, 5,498,772 fire occurrences, of 30m scale, were recorded during the sampling period (2005-2018), which were chiefly in the agricultural fields adjoining the forests and in the dry savannahs of the region. I derived the Euclidean distance from fire at the grain sizes used in the study, as fire can degrade nearby areas by spreading ashes and smoke that can support invasion (Hiremath & Sundaram 2005).

I obtained the forest loss data from the global forest cover loss (ver.2) for the period 2000-2017 (Hansen et al. 2013), which is available at 30 m scale. I derived Euclidean distance from the forest loss pixels at different grain sizes, as the forest opening are known to aid the spread of invasive plants at larger areas.

I derived the vegetation-browning index using a time series analysis on MODIS EVI 16-day interval product (250m resolution) from the year 2000 to 2018. In total, there were 432 temporal replicates for each pixel. I used harmonic regression that fitted the first-order Fourier model followed by the linear regression, which is similar to the BFAST algorithm. This, at first calculates the yearly average variation in the EVI and then the linear regression reduces it for yearly comparison to assess the increasing ('greening') or decreasing ('browning') trend for the pixel. This processing was done using the cloud-computing technology in the Google Earth Engine platform, which enables parallel and big data processing required for large study areas. Subsequently, I up-scaled the product at different grain sizes.

Effect of anthropogenic pressure

I use nighttime lights data from the Day/Night Band (DNB) on the VIIRS sensor, which is a panchromatic band that can detect very dim nighttime scenes. Nighttime light acts as an index of human density (Levin & Duke 2012), human development (Elvidge et al. 2012), greenhouse gas emissions and light pollution. These anthropogenic pressures are known to facilitate the spread of invasive plants globally and hence, I use them in place of quantitative disturbance index (e.g. number of trees cut, branches felled, people seen, etc.). This nighttime light were availed at ~250 m and subsequently upscaled at different grain sizes in consideration.

I procured a vector layer of railways and roads (national highways, state highways, all metaled and cart track roads) from the Survey of India. The road network ranks second largest in the world (National Transport Policy Development Committee 2013), while the railway network is the fourth longest. These linear infrastructures cut across the forests and ecologically important areas and are known to facilitate invasive plants spread. I further calculated the Euclidean distance from it at all grain sizes.

Species Distribution Modelling

To get an estimate of invasive plants distribution in areas not sampled by ground surveys I used Maximum Entropy (MaxEnt) (Phillips et al. 2006a), one of the most widely used algorithms for distribution modeling. MaxEnt calibrates environmental variables from species presence locations and compares them with a set of random sample locations from the study area (Presence-background model). It uses this calibrated relationship of species presence with environment variables to seek similar locations that would likely support the target species. The most unconstrained model developed is considered as the MaxEnt model.

I divided the presence data of each species into training (80%) and testing (20%) sets, using k-fold partitioning design, with k=5. I used each k-partitioned set, for every species, as an input data for MaxEnt. Subsequently, in order to avoid the autocorrelation within the input data, it was filtered so as to select only one presence point from a grain.

Statistically, MaxEnt is a presence-background model that compares the presence locations with available environmental space (Phillips & Dudı 2008). The range of background environment substantially influence the response curve and subsequent modeled distribution, which necessitates appropriate ecological criteria and sampling strategy to define the background (Elith et al. 2011b; Webber et al. 2011). Since I only consider forested landscapes for this study, background points were obtained only from the forested areas of India. I modeled the kernel density of the presence locations and used this surface to select background points. Within the forests of this surface, I randomly selected 10,000 points to estimate the background environment. Similar to the filtering of input data, only one background point was selected from a grain.

I used linear, quadratic, hinge and product features to generate the MaxEnt model with 100 replicates for each species. Any bias correction protocol was not required, as the data was systematically collected across the study area. Area Under the receiving operating characteristic Curve (AUC) of MaxEnt model was considered as an additional criterion to assess the ability of MaxEnt model to predict invasive plants presence. MaxEnt produces niche probability for every pixel that varies from 0 to 1. In the present study, all pixels of the output raster that were greater than a threshold that had highest True Skill Statistics (TSS), were considered as presence. To assess the TSS, I used the 20% test data retained initially and the true absence data recorded as that location, where the species has been absent consistently across the sampling period (2006-2018). I average the results of all the k-partitioned model runs, for each species. Subsequently, I compared the distribution estimate, model AUC, model TSS and contribution of predictor's response at different grain sizes. For summarizing the effects of change in grain size, I averaged the parameters for all species at each scale and subsequently compared the mean and variations.

To compare the effect of grain size on the distribution estimate, I use the range ratio, which is of ratio of area at larger grain to area at smaller grain (Franklin et al. 2013). I selected ratio scheme was 250 m vs. 500m, 250 m vs. 1 km, 250 m vs. 2 km, 250 m vs. 5 km, 250 m vs. 10 km and 250 m vs. 20 km. While, the ratio compared the distribution estimate, it does not produce information of the congruence between the two estimates i.e. two estimates might have same area, but geographically different. To address this, I use spatial congruence index (Franklin et al. 2013) on the same pairs selected for range ratio. spatial congruence index is calculated as $2x / (2x + y + z)$, where x is the common distribution area identified by two models, y is the distribution area identified at only smaller scale, z is the distribution area identified at only larger scale. Higher values of this index represent higher spatial similarity in the compared distributions.

Previous studies identified the source of changes in distribution to the nature of response curve that determine the distribution of species with respect to different predictors (Franklin et al. 2013; Connor et al. 2018). However, due to many species that have different response shape for each predictor, it becomes difficult to quantitatively assess the difference in the geometry of the shape. Hence, based on MaxEnt results, I selected significant and ecologically important predictors to compare the response curves at different scales by identifying the change in nature of curve (e.g. unimodal, monotonic, lower peak, response width).

Ensemble modeling

The covariates used to index the drivers of invasive species presence might have a natural scale of occurrence at which they were capture. For an example, annual rainfall in India was found to be spatially independent at 4 km^2 scale, below which it shows a substantial auto-correlation. Using covariates below their natural scale can distort the model and over-emphasize the influence of single variable. To address this bias, I derive the natural scale of spatial independence using Moran's I for each covariate used, at every scale. In order to get the relation of grain size and autocorrelation I estimated the Moran's I at additional grain sizes, thus comprising of 30 m, 100 m, 250 m, 500 m, 1 km, 2 km, 5 km, 10 km, 20 km and 40 km. The scale, at which the Moran's I was ≤ 0, was considered as the natural scale to account the variation within the predictor. After deriving the natural scale of each covariate, for all the resolution below it, I weigh each model (M), in which the covariate was used, negatively by the product of percent contribution (C) of the particular covariate and its standardized Moran's I coefficient (MI). After weighing every model by the natural scale of operation, I ensemble the multi-scale models for each species by deriving per pixel probability (ESD) based on its weight assigned by True Skill Statistics i.e. TSS (WTSS).

$$ESD = \sum_{scale=250}^{20000} \frac{(M)}{(\frac{C_1}{MI_1}) + (\frac{C_2}{MI_2}) + \cdots + (\frac{C_n}{MI_n})} X\ (WTSS)$$

Results

The performance of MaxEnt models varied across species and grain sizes. The AUC values decreased as the log of grain size increased, more drastically (slope = -7.3, $R^2 = 0.98$, $p < 0.001$) for specialist herb species i.e. species occurring in a single type of forest type (*Ageratina adinophora, Ageratum conyzoides, Mimosa diplotrica,* and *Xanthium strumarium*), than for generalist herb species (i.e. species occurring in multiple forest type) (slope = -7.2, $R^2 = 0.96$, $p < 0.001$) (*Chromolaena odoratum, Hyptis suaveolens, Parthenium hysterophorus, Mikania micrantha* and *Senna tora*), which were drastic than shrub species (slope = -7, $R^2 = 0.80$, $p < 0.05$) (*Lantana camara* and *Prosopis juliflora*). The TSS increased for nine out of eleven species from 250 m to 1 km and then declined with the increase in grain size. The two species left were shrubs (*Lantana camara* and *Prosopis juliflora*), which had gained in TSS from 250 m to 5 km and then a decline (figure 13).

The average permutation importance of every predictor across, and at each grain size is provided in Table 7. When average of each predictor contribution for all species was assessed, it was found varying from smaller scale to larger scale. It increased significantly for mean rainfall (slope = 16.5, $R^2 = 0.99$, $p < 0.001$), maximum temperature of warmest month (slope = 14.7, $R^2 = 0.99$, $p < 0.001$), mean temperature of coldest quarter (slope = 11.7, $R^2 = 0.99$, $p < 0.001$), and mean rainfall of driest month (slope = 17.4, $R^2 = 0.98$, $p < 0.001$). It decreased significantly for deciduousness (slope = -5.9, $R^2 = 0.99$, $p < 0.001$), vegetation browning (slope = -10.6, $R^2 = 0.98$, $p < 0.01$), nightlight (slope = -7, $R^2 = 0.96$, $p < 0.01$) and distance from infrastructure (slope = -14.9, $R^2 = 0.99$, $p < 0.001$). It insignificantly decreased with distance from water (slope = -10, $R^2 = 0.97$, $p <$

0.01), canopy cover (slope = -5, $R^2 = 0.99$, $p < 0.001$), distance from fire (slope = -5.5, $R^2 = 0.97$, $p < 0.01$) and distance from forest loss (slope = -5.9, $R^2 = 0.98$, $p < 0.05$).

In general, the nature of response curves shifts from small range to broad range with increase in the grain size. Figure 14 shows the difference in response of *Mikania mcrantha* presence to four significant predictors; maximum temperature of warmest month, annual rainfall, forest moistness and vegetation browning. In general, the nature of response curve remained consistent with climatic predictors for most of the species, but the associated deviations expanded in the intermediate grain sizes. In case of the response curves for biotic predictors, their shape changed significantly across the grain sizes, with more precise deviations at smaller grain sizes.

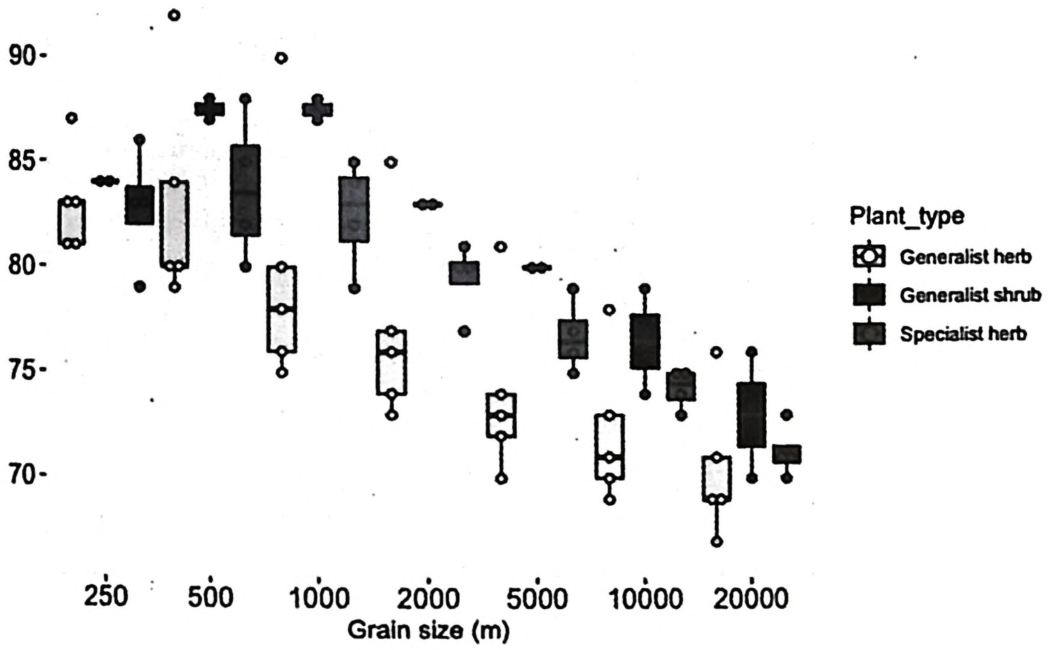

Figure 15 Effect of grain size on TSS: The variation in standardized TSS against the log of the grain size used (i.e. 250 m, 500 m, 1 km, 2 km, 5 km, 10 km and 20 km).

Table 7 Effect of scale on covariate contribution: Mean permutation contribution of environmental predictors to the distribution of 11 invasive plants at different scales (Range of the permutation contribution). Gradient of darker grey represent higher contribution of the covariates.

Scale	Mean R	Driest R	Max T	Cold T	Water	Canopy	Decid	Fire	Brow	F loss	NightL	Infra D
250	1.5	3.2	2.2	0.7	20.6	16.3	14.8	10	20.5	12.6	14.3	31.7
	(0 - 3)	(1 - 7)	(0 - 6)	(0 - 1)	(9 - 32)	(9 - 24)	(10 - 18)	(5 - 16)	(15 - 29)	(4 - 21)	(9 - 20)	(14 - 44)
500	4.9	6.2	5.1	2.2	19	14.3	13.8	9.3	18.3	11.6	11	30.1
	(1 - 8)	(2.2 - 10)	(3 - 9)	(1 - 4)	(5 - 36)	(11 - 20)	(8 - 18)	(3 - 18)	(12 - 25)	(3 - 19)	(6 - 15)	(16 - 38)
1000	11.3	13.2	9.7	6.7	14.4	13.3	11.8	7.5	12	10.1	8.1	25.9
	(3 - 20)	(5 - 21)	(4 - 17)	(2 - 12)	(3 - 33)	(9 - 17)	(5 - 16)	(3 - 14)	(9 - 16)	(2 - 18)	(3 - 11)	(14 - 33)
2000	17.6	22.2	15.4	11.2	9.5	11.3	9.2	4.5	9.5	8.4	6	19.4
	(4.5 - 27)	(14 - 29)	(8 - 27)	(4 - 16)	(1 - 28)	(6 - 14)	(1 - 14)	(3 - 8)	(8 - 12)	(1 - 15)	(3 - 10)	(8 - 26)
5000	23.1	25.8	21.9	14.3	6.9	9.5	7.8	2.5	6.5	6.1	3.1	13.5
	(10 - 33)	(16 - 32)	(10 - 30)	(5 - 19)	(0 - 25)	(3 - 18)	(1 - 11)	(2 - 4)	(5 - 8)	(1 - 13)	(2 - 7)	(6 - 20)
10000	28.1	30.6	25.2	18.8	4.6	7.5	5.8	1	2.8	3.9	1.9	8.9
	(18 - 38)	(18 - 36)	(13 - 35)	(9 - 27)	(0 - 21)	(0 - 19)	(0 - 10)	(0 - 2)	(2 - 4)	(0 - 8)	(1 - 4)	(2 - 16)
20000	31.5	35.2	28.8	22.2	2.9	7	3.8	0.8	0.8	1.4	1	5.5
	(20 - 40)	(23 - 43)	(15 - 38)	(10 - 30)	(0 - 15)	(0 - 20)	(0 - 10)	(0 - 2)	(0 - 2)	(0 - 4)	(0 - 3)	(0 - 9)

Mean R: mean rainfall, Driest R: rainfall of the driest season, Max T: maximum temperature of warmest month, Cold T: mean temperature of coldest quarter, Water: distance from water, Canopy: canopy cover, Decid: deciduousness of the forest, Fire: distance from fire, Brow: vegetation browning index, F loss: distance from forest loss, NightL: night time lights, Infra D: distance from infrastructure

The distribution area, based on the TSS, for each species at every scale is provided in Table 8. The distribution estimate increased for all species from 250 m to 20 km grain size. When compared with the true distribution at 5 km grain size, the predicted distribution was always greater with the lowest difference ($p < 0.05$) for specialist herb species (*Ageratina adenophora, Ageratum conyzoides, Mimosa diplotricha,* and *Xanthium strumarium*), moderate for generalist herb species ($p < 0.05$) (*Chromolaena odorata, Hyptis suaveolens, Parthenium hysterophorus, Mikania micrantha* and *Senna tora*), and highest for shrub species ($p < 0.1$) (*Lantana camara* and *Prosopis juliflora*).

The range ratio increased with grain size (figure 15), particularly for specialist and generalist herb species, then that for shrub species. Generally, the range ratio was similar till gain from 250 m to 1 km and increased substantially after that for herbs, while it increased substantially only after 5 km for shrubs. The spatial congruence index decreased with increase in the grain size, with 80% similarity till 1 km for herbs, and till 5 km for shrubs (figure 15).

The spatial autocorrelation in different covariates, as indexed by Moran's I, is provided in Table 9 and figure 16. It was observed that climatic covariates become independent above 2-5 km, while resources and biotic covariates become independent above 0.5-1 km. The multi-scale ensemble model provided the best classification of all invasive plants when the TSS of each species at every scale was compared with the TSS of its ensemble model (figure 17). The ensemble model produced visually most correct map of few invasive plants, for which regional high-resolution distribution was availed from secondary data[1] (figure 18). Similar maps for all invasive plants are provided in figure 19.

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[1] Two high resolution maps of *Lantana camara* was generously provided by Merwyn Fernandis (for Rajaji Tiger Reserve) and Rajat Rastogi (for Kanha Tiger Reserve), from their PhD and Master's thesis respectively.

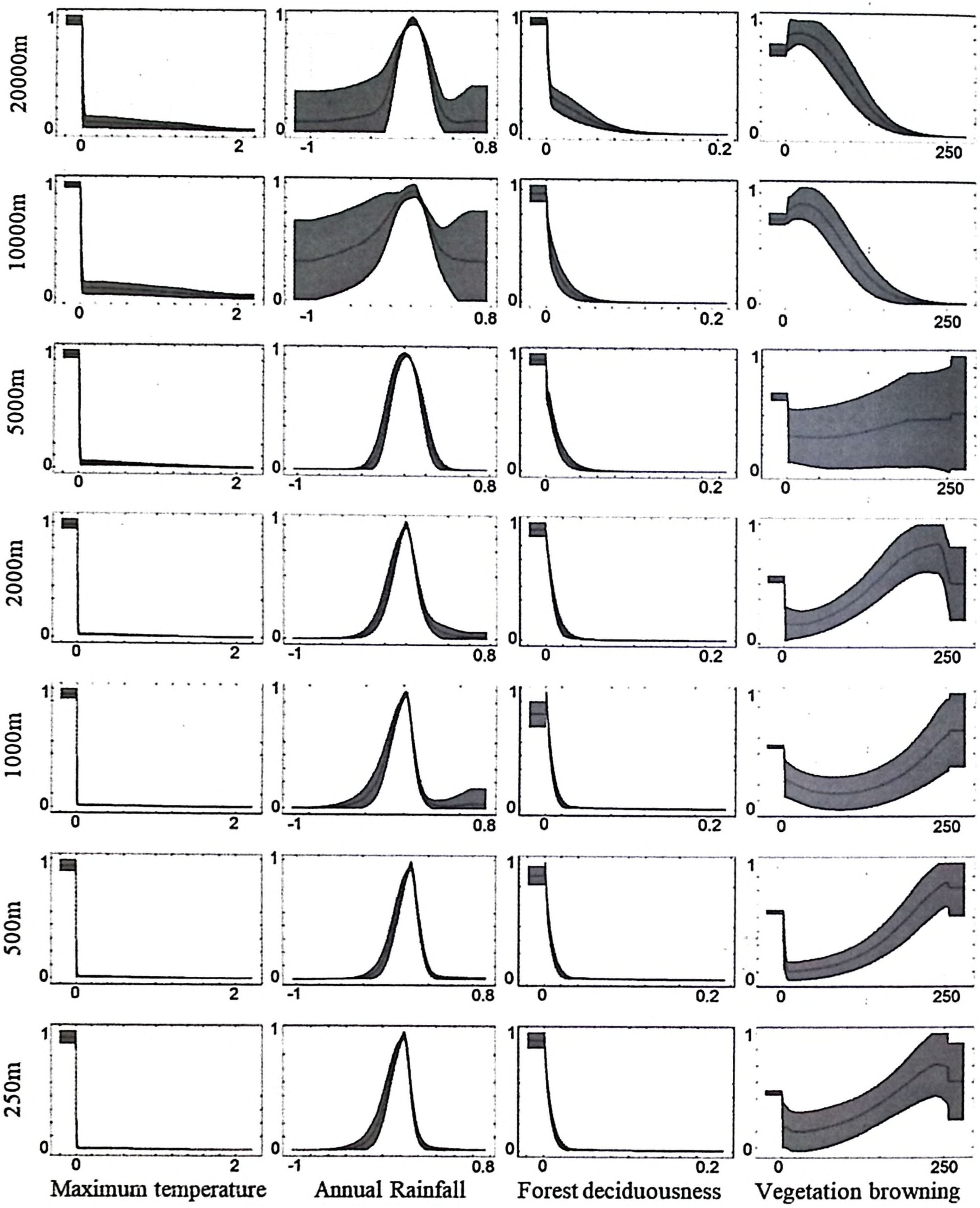


Figure 16 Scale-specific response of invasive plants: An example of invasive *Mikania micrantha* showing differential response (Y-axis: Occurrence probability) to environmental predictors (X-axis) at different grain sizes. While the response to climatic variables remained consistent across the scales, response to biotic variable changed with scale and was ecologically relevant at smaller grain sizes.

Table 8 Invaded area: Area on distribution (km^2) modelled at various grain sizes for 11 invasive plants in India.

Species	250	500	1000	2000	5000	10000	20000
Ageratina adinophora	98,032	126,879	142,985	168,204	200,896	219,875	226,104
Ageratum conyzoides	67,550	90,165	125,360	137,940	149,003	177,604	200,105
Chromolaena odorata	88,891	110,364	125,046	139,246	160,579	182,640	212,364
Hyptis suaveolens	80,549	100,568	119,460	134,879	145,267	160,236	182,468
Lantana camara	221,657	258,965	294,530	300,054	303,607	349,069	410,059
Mikania micrantha	90,765	116,284	132,689	151,268	172,304	198,801	201,267
Mimosa diplotricha	70,464	92,549	106,204	114,730	130,945	148,921	157,346
Parthenium hysterophorus	95,784	121,498	154,730	199,527	209,459	227,896	262,743
Prosopis juliflora	106,034	133,087	197,058	201,463	222,284	256,987	314,379
Senna tora	105,111	126,502	142,674	181,298	208,573	245,793	299,604
Xanthium strumarium	41,564	68,512	98,067	109,245	115,264	124,567	139,645

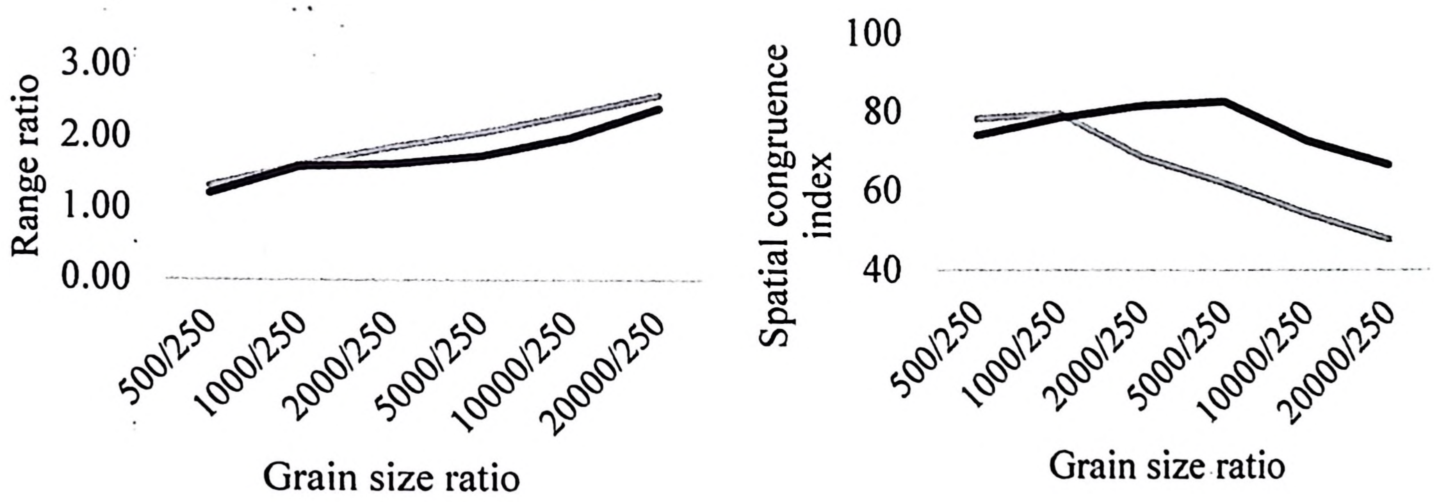


Figure 17 Variation in range ratio (a) and spatial congruence index (b) with respect to increasing grain size ratio (250 m vs. 500m, 250 m vs. 1 km, 250 m vs. 2 km, 250 m vs. 5 km, 250 m vs. 10 km and 250 m vs. 20 km).

Table 9 Natural scale of spatial independence: Spatial auto-correlation estimated using the Moran's I coefficient for different environmental predictors at different scale. Bold values represent spatially independence of the variable.

Covariates	**30m**	**100m**	**250m**	**500m**	**1000m**	**2000m**	**5000m**	**10000m**	**20000m**	**40000m**
Maximum temperature of warmest month	0.943	0.916	0.747	0.289	0.148	**0.002**	**-0.043**	**-0.094**	**-0.296**	**-0.513**
Mean temperature of coldest quarter	0.989	0.915	0.571	0.310	0.197	0.024	**-0.034**	**-0.116**	**-0.322**	**-0.589**
Mean rainfall	0.933	0.888	0.701	0.435	0.247	0.067	**-0.106**	**-0.192**	**-0.305**	**-0.606**
Rainfall of driest season	0.813	0.796	0.647	0.394	0.182	**-0.004**	**-0.122**	**-0.397**	**-0.460**	**-0.725**
Distance from water	0.861	0.216	0.016	**-0.115**	**-0.254**	**-0.311**	**-0.410**	**-0.515**	**-0.698**	**-0.862**
Canopy cover	0.582	0.113	0.024	**-0.065**	**-0.104**	**-0.155**	**-0.214**	**-0.437**	**-0.660**	**-0.776**
Deciduousness of the forest	0.625	0.197	0.087	0.001	**-0.064**	**-0.202**	**-0.293**	**-0.413**	**-0.666**	**-0.784**
Vegetation browning	0.212	0.072	**-0.015**	**-0.147**	**-0.261**	**-0.335**	**-0.423**	**-0.606**	**-0.811**	**-0.874**
Distance from fire	0.811	0.382	0.141	0.034	**-0.075**	**-0.135**	**-0.256**	**-0.312**	**-0.410**	**-0.522**
Distance from forest loss	0.921	0.593	0.205	**-0.002**	**-0.106**	**-0.194**	**-0.303**	**-0.496**	**-0.574**	**-0.722**
Nightlight	0.730	0.502	0.107	**-0.043**	**-0.184**	**-0.302**	**-0.369**	**-0.601**	**-0.799**	**-0.883**
Distance from infrastructure	0.216	0.047	**-0.194**	**-0.315**	**-0.411**	**-0.580**	**-0.633**	**-0.722**	**-0.852**	**-0.920**

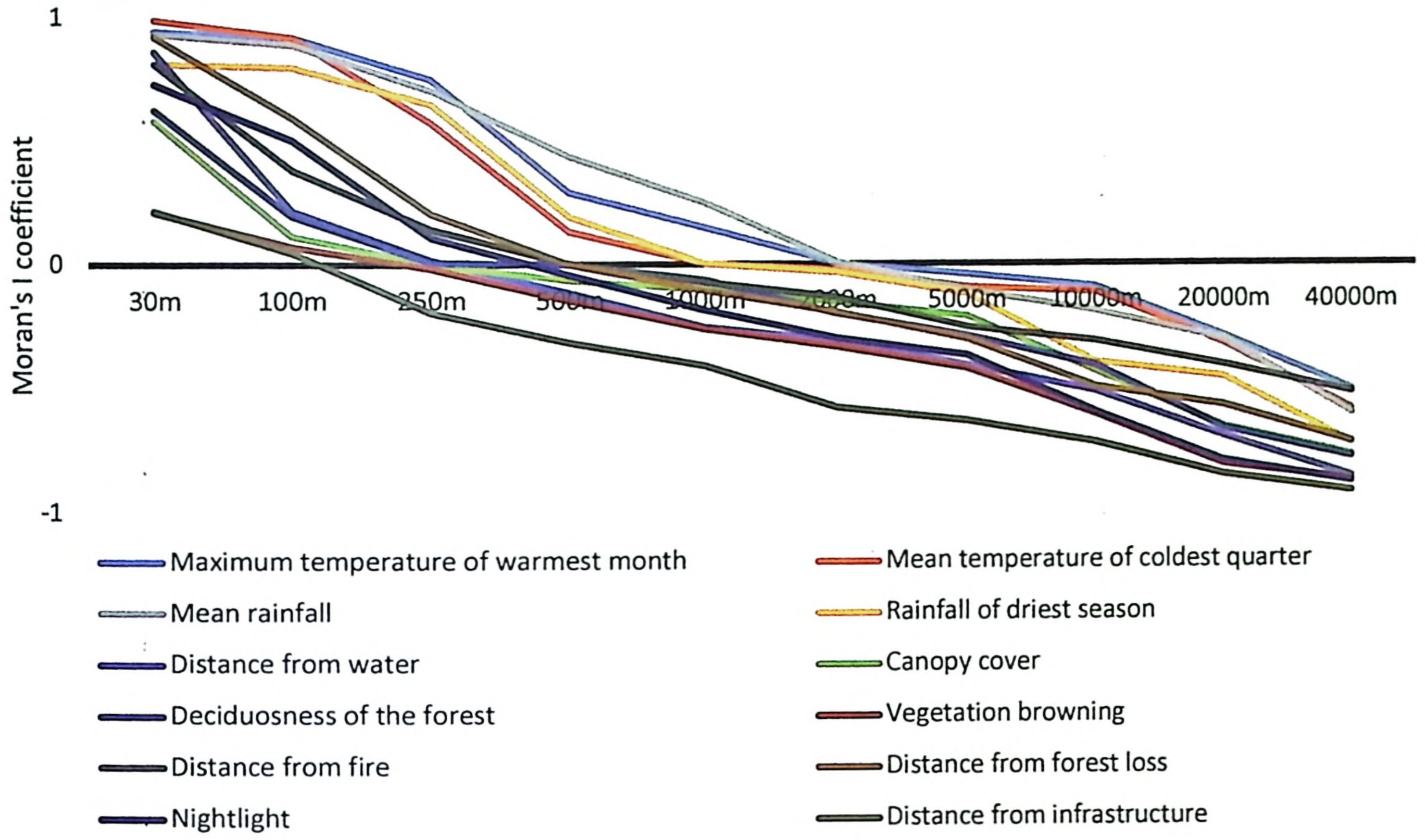


Figure 18 Moran's I: Spatial auto-correlation estimated using the Moran's I coefficient for different environmental predictors at different scale.

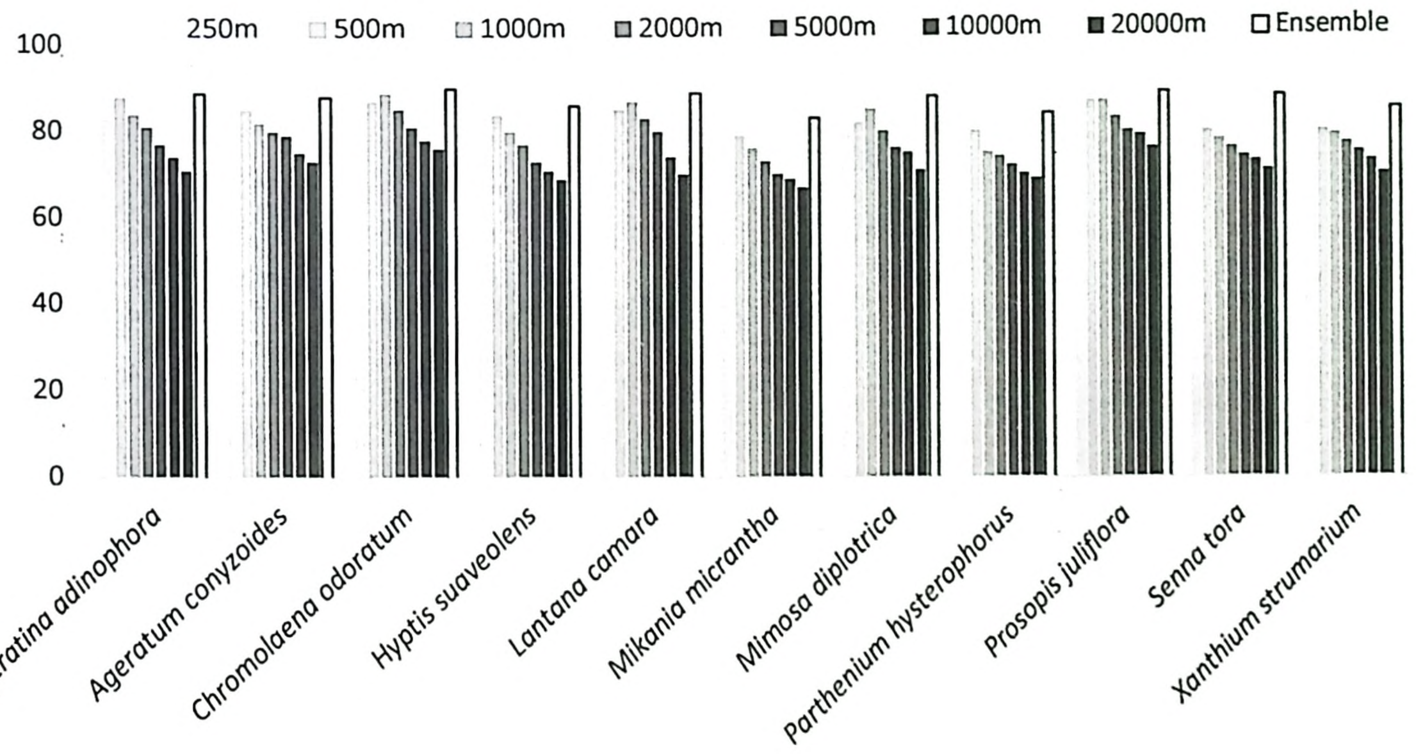


Figure 19 Accuracy of multi-scale models: Comparing the percent standardized True Skill Statistics (TSS) for different species at different scale revealed the multi-scale ensemble model to consistently accurate for classifying species presence

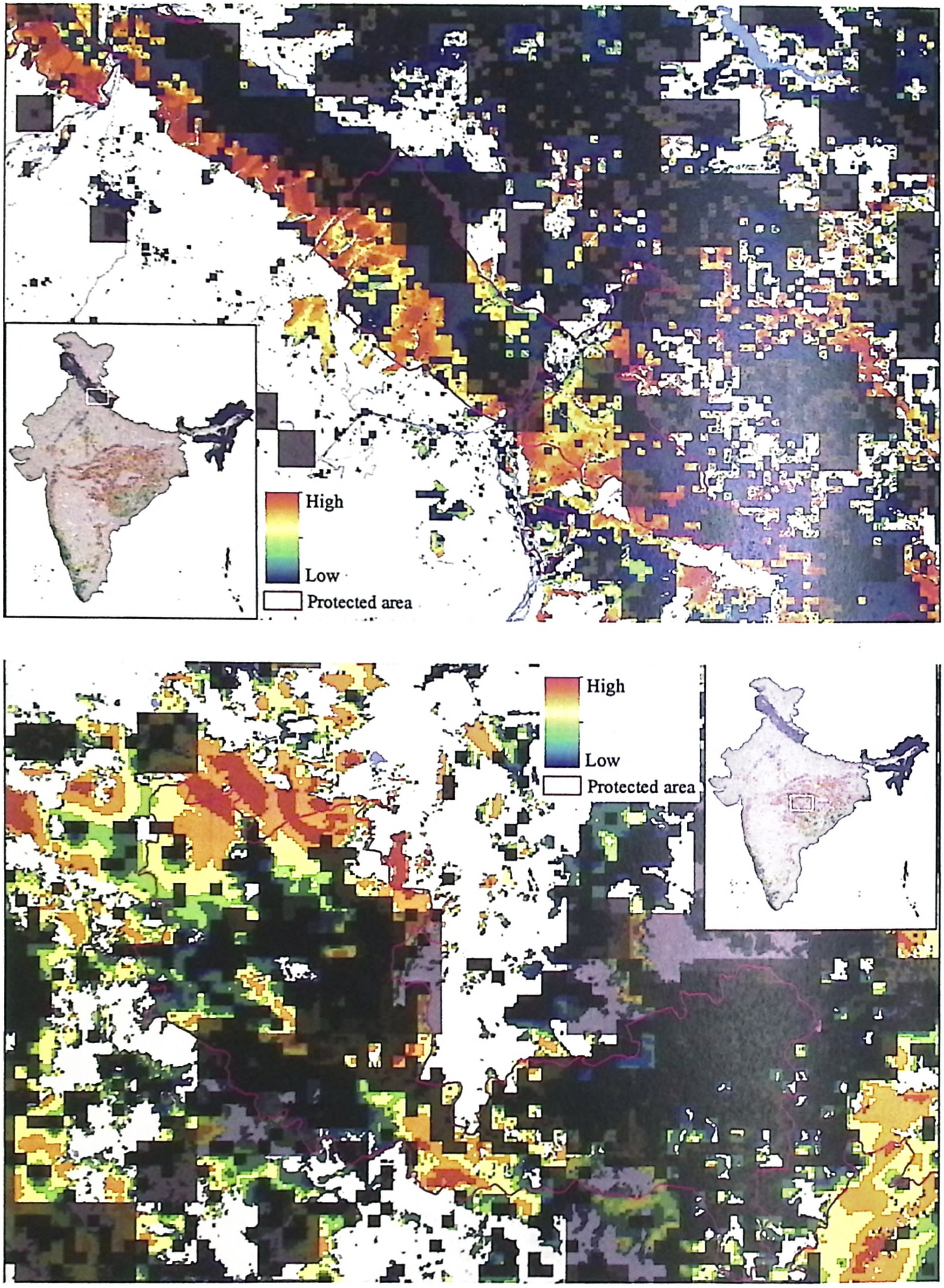
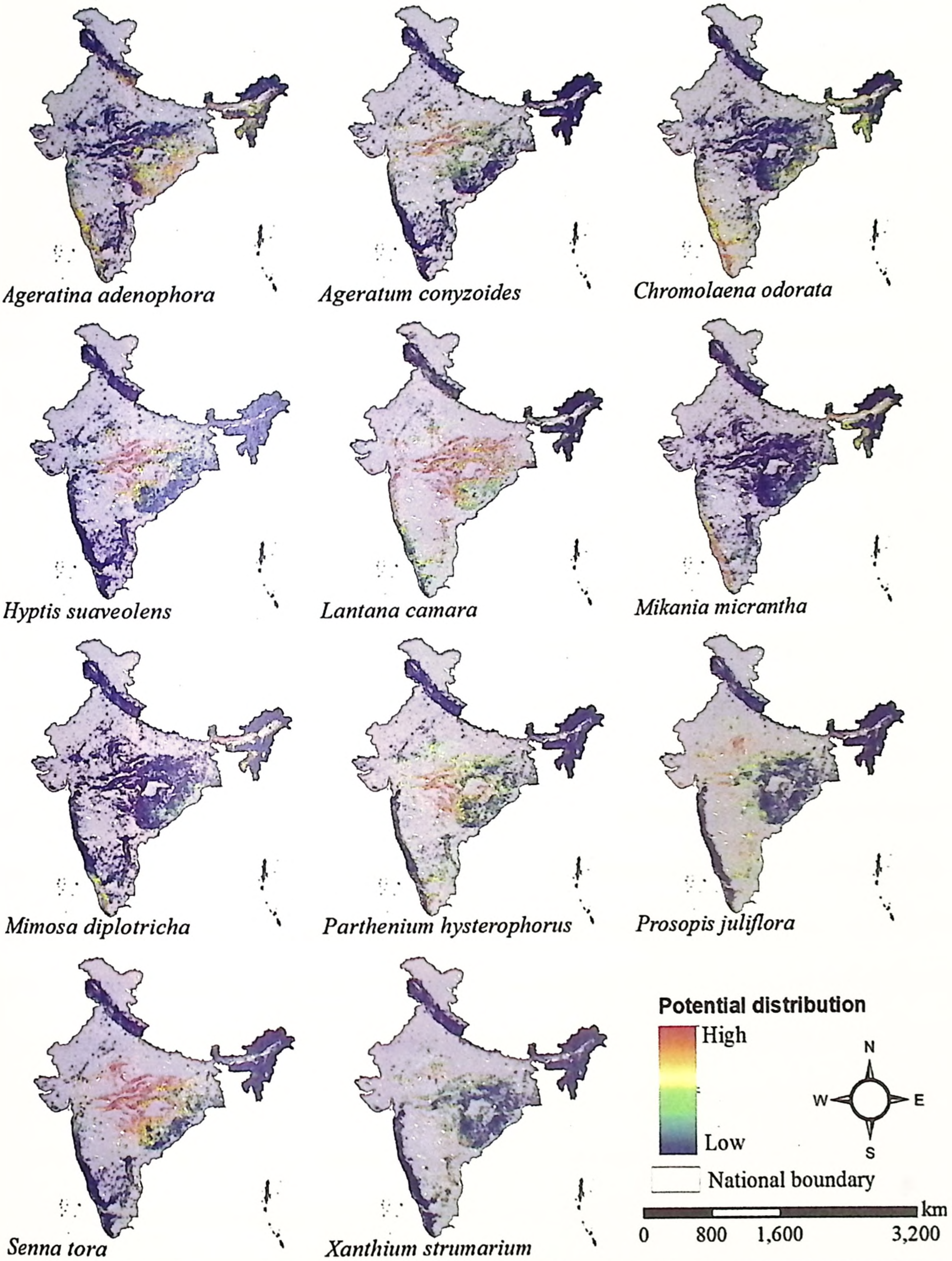


Figure 20 Multi-scale ensemble drivers of invasive plants: Example of Multi-scale ensemble model of *Lantana camara* for India (inset), highlighted for Rajaji Tiger Reserve and Kanha Tiger reserve. Larger dark pixels represent the influence of climatic parameters, which are significant only above 2 km^2 scale. While at smaller pixel size, the influence of other biotic parameters is relatively significant.



Ageratina adenophora

Ageratum conyzoides

Chromolaena odorata

Hyptis suaveolens

Lantana camara

Mikania micrantha

Mimosa diplotricha

Parthenium hysterophorus

Prosopis juliflora

Senna tora

Xanthium strumarium

Figure 21 Invasive species distribution: Multi-scale ensemble model for all High Concern Invasive plants in India, derived from distribution at various grain size (250m, 500m, 1 km, 2 km, 5 km, 10 km and 20 km)

Discussion

The distribution estimate of species varies in magnitude and geographically across the grain sizes, with the estimate, generally, increasing with grain size. This could be because, at small grain sizes the models were contributed by disturbance and resource attributes that vary significantly across the landscape. While, the large grain size models were contributed by climatic attributes, which vary at macro-scale. Hence, larger grain size model might have predicted an area as suitable for distribution, which in reality might lack the resources required for species to invade, at first. However, the range ratio was observed to increase with the grain size, which can be result of the large-scale distribution of species, where the species has mostly extended across its potential extent.

I found that model parameters vary with the species in consideration. The AUC that considers presence-background comparison decreased with increasing grain size, more for specialist herbs than for generalist herbs, which was more than for generalist shrubs. Greater accuracy at modeling specialist species was also found in earlier studies (Connor et al. 2018). The TSS that takes in consideration the strength of a model to classify presence as presence and true absence as absence increased from small grain size (250 m) to moderate grain size (1 km for herbs, 5 km for shrubs) and then substantially decreased. This was observed to be greatly influenced by the absence of species, which determines the specificity of the model. The absence of herbs is specific to high canopy area, with either preference or avoidance to deciduousness of the forests and mostly within the disturbed habitats. These parameters change significantly only around a scale of 1 km. While, the absence of invasive shrubs was not specific to such disturbance-forest attributes, but mostly specific to climatic and broader hydrological predictors, which change at macro-scale. Moreover, these shrubs are known to spread by vegetative propagation, and are adaptive in resource utilization, hence, they might initially depend on the small-scale disturbance that avail resources from the native forests and then invade irrespective to the forests and resource attributes.

I confirm that restricting the SDMs to include only coarse-scale climatic data may improve our knowledge on the influence of climatic parameters on the species; however, it impedes our understanding on 'why a species is present at a particular site?' Moreover, is of little contribution to understand how anthropogenic disturbances drives invasive species spread. I found that the effect of anthropogenic disturbances and resources was markedly significant at small grain size; however, the contribution of climatic parameters was lowest there. Hence, if a model is desired at an optimal scale, which could take in consideration the effects of all the important landscape drivers, I show it would be at from 1 to 5 km grain size.

There is a growing demand amongst ecologists, climate scientists and conservationists to understand the scale at which landscape changes are influencing invasive species. The usual SDMs based protocol to decipher the multi-scale effects, trained on virtual species or opportunistically collected data, help only to highlight the necessity of large-scale systematic data for validity. Based on the largest known systematic sampling for invasive species, our results, for first, suggests that invasive plants, are generally facilitated by small-scale (250 m, 500 m, 1 km) anthropogenic disturbances (infrastructural disturbances, vegetation browning, forest loss, and fire) and resource attributes (water availability, deciduousness and canopy cover); and large-scale (1 km, 2 km, 5 km, 10 km and 20 km) climatic parameters (mean rainfall, rainfall of the driest quarter, maximum temperature of warmest month and mean temperature of winters). While doing so, it is essential to consider the natural scale of covariates considered. For an example, in the present study, climatic parameters that vary only above 2 km, were found to be significantly important contributors to species distribution at smaller grain size. This was product of the auto-correlation bias, due to which the distribution model was influenced by single covariate that skewed the contribution and response to other covariates. Hence, while comparing species distribution or species' response at multiple scales, it is crucial to either exclude the spatially auto-correlated covariates or weigh them negatively by the coefficient of autocorrelation. Multi-scale ensemble model used in the present study is the first case where multi-scale distribution models are ensemble used an index of spatial independence, and serves a greater opportunity for the field of biogeography and distribution modelling. This ensemble availed us to model the most accurate species distribution as compared to any individual scale, and helped us understand the influence of nested landscape drivers in spread of invasive plants.

Invasive plants have substantially invaded different forests across India, with preference to forests that are fragmented (forest loss) due to infrastructural activities or fire, and are degrading in terms of cover (vegetation browning) due to local or global changes. One of the highest human population densities, which is consistently developing, surrounds Indian forests, particularly in the tropics. This demands a quintessential infrastructural growth, promised by recent governments, particularly in terms of road networks, built-up areas, etc. Our study found invasive species of all kinds i.e. specialist herbs, generalist herbs and generalist shrubs, facilitated by small-scale disturbances that either causes loss in forest area or degradation of the forest quality. Our models also suggest that either of the invasive plants might have already invaded almost 90% of the tropical forest. The least invaded forests were found in the parts of Western Ghats, Central Indian Eastern Ghats, and Northeastern hills; which are currently being considered for major land use land cover changes. Our model suggests that such changes can substantially risk the forest of invasion, if the change is greater than 1 km^2. Finding of the current study can be used in these forests to prioritize important conservation area, so as to keep human footprint below the scale of risk. These finding also have global relevance, particularly for tropical developing countries that harbor higher biodiversity and larger rate of land use change.

CHAPTER 6: THE SPREAD OF INVASIVE PLANTS

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Introduction

Invasive species proliferate as a response to the absence of competition and predation from the native species, adaptive plasticity, etc. (Suarez & Tsutsui 2008). Anthropogenic disturbances facilitate invasive species by creating an environment, where the competition from the native species is reduced or the phenotypic plasticity of an invasive species is triggered (Mungi et al. 2018). While anthropogenic disturbances have direct effect on invasive species, climate change has an indirect effect on the spread of invasive species. The competition from native species would be weakened due to climatic stress, and invasive species could take an advantage. This has been documented in various taxa globally (Dukes & Mooney 1999; Stachowicz et al. 2002; Walther et al. 2002; MacIsaac et al. 2011; Evans et al. 2016).

While the effects of these stressors are not completely independent, it is important to understand the contribution of each stressor so as to prioritize management actions to control them timely. However, one big reason for limited understanding on these questions is the absence of evidence based on long-term large-scale monitoring of the landscape. Invasive species are known to respond independently to these parameters in different geographies (chapter 4). And in the absence of large sampling scheme, it is difficult to understand the variation in their responses to the landscape characteristics, which could be the reason of why climate change, anthropogenic disturbances and invasive species are often considered in isolation. Absence of large-scale data not only delays management actions, but also hampers the scientific theories and hypotheses.

One such long-monitoring monitoring program that can help understand the dynamics of invasive species, climatic changes and anthropogenic disturbances is the one conducted in India (chapter

3). These forested areas are further being fragmented by the infrastructural development happening in the country, which is expected to increase in the wake of imminent economic development (Ravindranath et al. 2012). While anthropogenic disturbances are increasing in the region, with degrading forests and high invasion magnitude, the global climatic changes are affecting the key temperature-precipitation regimes in the region. The monsoon in the north-central regions of India has been declining (Salzmann and Cherian 2015), while the winter temperature is lower Himalaya is getting warmer (Sharmila et al. 2015). Thus, it is pertinent to know how climate change and anthropogenic disturbances are influencing biological invasions in these tropical forests. In fact, this is the single known data, where the empirical validation for these interactions could be tested due to the largest spatio-temporal replication.

The effects of climatic changes, anthropogenic modifications and management manipulations are spatially heterogeneous and depends on the ecosystem type. To understand how these spatially explicit changes affect the invasion of plants, it is essential to independently study these ecosystems. For an example, it is established that warming winters, loss of moisture and over-grazing in the moist forest systems are facilitating plant invasions (e.g. Joshi et al. 2020, Mungi et al. 2020, 2018); whereas gain in moisture and reduced grazing are facilitating woody invasions in drier and mesic savannas (e.g. Ratnam et al. 2019, Prasad et al. 2018, Sankaran et al. 2005). To test these ecological patterns, I used the presence of 11 high concern invasive plants in India in a dynamic occupancy framework (MacKenzie et al. 2003) based on the hypotheses that a) invasive plants of the moist forests are facilitated by warming climate, low rainfall, forest degradation and loss of moisture in the area. b) Invasive plants of the drier forests are facilitated by higher rainfall, increased moisture in the area, infrastructural growth and grazing by livestock. c) Irrespective of the species, the probability of invasion in neighboring areas of invaded regions is higher.

Method

Sampling design:

I selected the presence data of all 11 high concern invasive plants from a consistently sampled grids in 2006, 2010, 2014 and 2018. By using species richness curve I estimated that for covering the invasive flora in a grid of 5x5 km, it must have minimum 8 plots in the Shivalik-Terai landscape, 5 plots in the central Indian landscape, 12 plots in the Western Ghats landscape and 16 plots in the Northeastern landscape. This constituted a repeated survey of 82,450 km2 forests at the scale of 25 km2, in 12 years. Within the same sampling frame, I enumerate the site covariates, which I hypothesized would influence the occurrence of invasive plants in the area. Details of all covariates is provided below.

Distance from previously invaded areas:

Invasive species like *Lantana camara*, *Mikania micrantha* and *Ageratina adenophora* are known to propagate vegetatively, while plants like *Prosopis juliflora*, *Senna tora* and *Xanthium strumarium* are known to be locally dispersed by different dispersal agents. Thus, the likelihood of an area adjoining invaded site to get invaded by these plants is higher as compared to the area where the species dispersal is difficult. To include this dispersal parameter in the dynamic occupancy mode, I calculated the Euclidean distance of each grid from the nearest invaded grid for each sampling year, and used it as a covariate of nearness to invaded sites in the successive occupancy model.

Water availability:

Water forms a primary requirement for growth of many plants, including the invasive plants. In Indian tropical forests the primary source of water at large scale is the annual rainfall that regulate the water catchments and hydrological flux in an area. Indian rainfall has been shown to vary in last three decades as a consequence of the ongoing global climatic changes. This can not only influence the hydrological dynamics of the forests but also degrade the forest in the long run. I used the annual rainfall observation provided by the Indian Meteorological Department. I calculated the rainfall normal for the time window of 2003-2006, 2006-2010, 2010-2014 and 2014-2018. This data was downscaled using the PRISM technique to 5x5 km scale, and used as an index of water availability in the area.

Secondly, I considered the water deficit of an area, because an area might receive higher rainfall but the subsequent temperature driven transpiration might exhaust the water. Hence, how long the groundwater generated by rainfall would be availed for use can be indexed by the water deficit index. I used the climate water deficit, derived using a one-dimensional soil water balance model for the year 2006, 2010, 2014 and 2018 for modelling the spread of invasive plants.

Climatic temperature:

Temperature, particularly during the post-monsoon seasons in tropical India is important for the growth of many plants. Higher temperature and shorter winter months coincide with the vegetation types where senescence appear early, as compared to the vegetation type where senescence is delayed (e.g. moist deciduous forests, semi-evergreen forests) (Shreshtha et al. 2012). Hence, I used the normal average temperature provided by the Indian Meteorological Department for the month of December, January and February for the time window of 2003-2006, 2006-2010, 2010-2014 and 2014-2018. This data was downscaled using the PRISM technique to 5x5 km scale, to use in the occupancy models.

Forest edge density:

Fragmentation of the forest is known to facilitate the spread of invasive plants, due to reduced competition and unutilized resources. There are different ways through which forest fragmentation could be indexed, I used the structural fragmentation. For doing this I used the forest layer provided by the Forest Survey of India in 2014 and calculated the length of each path in a grid. Further, to incorporate the fragmentation caused by roads and railways, I used the length of intersection of roads and railways with the forest in a grid (obtained from the Survey of India, for 2001 and 2011). I also added the intersection of rivers (obtained from the Survey of India, for 2001 and 2011) with the forest in the grid. Furthermore, I obtained the forest loss data from the global forest cover loss (ver.2) for the period 2000-2006, 2006-2010, 2010-2014 and 2014-2018 (Hansen et al. 2013), which is available at 30 m scale. And calculated the perimeter of the lost patch in a grid. Subsequently, I added the length of the forest edge, road and railway fragmentations, water channel fragmentation and forest lost perimeter in the grids to derive the forest edge density that was used as an index of forest fragmentation.

Forest cover change:

Including the changing forest cover was important considering that global and regional changes are known to degrade the forest structure gradually, which facilitates the spread of invasive plants. Secondly, greening in India is majorly due to agricultural expansion and plantation drives in the drier regions, which can potentially alter the micro-ecological process and influence the spread of invasive plants. As explained in chapter 5, I derived the vegetation greening-browning index for India using a harmonic regression that fitted the first-order Fourier model followed by the linear regression, on MODIS EVI 16-day interval product (250m resolution) for the year 2000-2006, 2006-2010, 2010-2014 and 2014-2018. Greening represents linear increment in the vegetation cover, while browning indicated loss.

Fire:

Similar to chapter 5, I obtained information on fire occurrence from the Fire Information for Resource Management System (FIRMS) database, which consisted of daily MODIS hotspots (Giglio et al. 2003) and Visible Infrared Imaging Radiometer Suite (VIIRS). In total, 5,498,772 fire occurrences were recorded during the sampling period (2000-2006, 2006-2010, 2010-2014 and 2014-2018), which were chiefly in the agricultural fields adjoining the forests and in the dry savannahs of the region. I derived the Euclidean distance from fire weighed by total number of fires in a grid, as fire can degrade nearby areas by spreading ashes and smoke that can support invasion (Hiremath & Sundaram 2005).

Urbanization index:

Similar to chapter 5, I used nighttime lights data from the Day/Night Band (DNB) on the VIIRS sensor, which is a panchromatic band that can detect very dim nighttime scenes.

Timber extraction:

In tropical India, people are dependent on forest timber for livelihood as well as commercial purposes. This extraction can reduce the competition from native trees to invasive plants and is important to be accounted in their spread. This extractive dependency could be at a small scale, which is not accounted in remotely sensed data and is hence important to be recorded on the ground. Across the sampling cycles, on every plot of vegetation sampling, where invasive plants were recorded, I also recorded number of trees fell and number of branches lopped. I averaged the total number of trees and branches fell across all the plots in a grid to index the pressure of timber extraction on the forest in the grid.

Livestock grazing:

India leads the world in the density of livestock, which chiefly uses savannah and dry forests as pasture lands since historical times. While grazing has been believed to maintain the regeneration in savannah and dry forests, its increased intensity in the face of rapidly depleting extent of natural vegetation across India can have negative consequences. Livestock grazing has been considered as a major driver for depletion in the native vegetation across the different conservation plans in India. In order to understand the effect of livestock grazing on the native forests, on every vegetation plot, a belt transect of 2m x 20m was laid to count the number of livestock dung. This was done for each sampling period. I averaged the total number of dung across all the plots in a grid to derive index the livestock grazing pressure on the forest in the grid.

Analysis:

In order to include the difference in species response across the biogeographic realms, I independently analyzed the spread for all species in the dry forests and moist forests. The difference in dry and post forest was made using the ratio of annual precipitation and temperature, which provides an index of aridity. Thus, I operated two models for every species that occurred in both forest types. Dynamic occupancy model, also called as multi-season occupancy model (MacKenzie et al. 2003), has been popularly used to learn about the change in distribution of species over long time. MacKenzie et al. (2003) described a basic Markov model to assess changes in occupancy status of a site (ψ) over seasons or years, which provides sufficient time for species occupancy to change. The model required two vital parameters, probabilities of local extinction and local colonization:

Extinction probability $\varepsilon i,t$ = Pr (area i not occupied in season t + 1 | occupied in t),

Colonization probability $\gamma i,t$ = Pr (area i occupied in season t + 1 | not occupied in t),

The underlying process model for occupancy dynamics was given as follows:

$$\psi_{i,t+1} = \psi_{i,t}(1 - \varepsilon_{i,t}) + (1 - \psi_{i,t})\gamma_{i,t}.$$

Here, the probability of area i being occupied at time t + 1 is the sum of two products: probability of persistence and probability of occupancy at i on t, and probability of colonization and probability of i being not occupied on t. However, these parameters (ψ, γ and ε) can also vary due to the placement of plots in a grid. While the grid might be occupied by the species, the plots might not essentially be occupied. The dynamic occupancy model addresses this detection bias (P) for every year. I further model these parameters as a function of the aforementioned site covariates. I created detection histories of detection (1) and non-detection (0) of all invasive plants across each of the consistently sampled grids. I modelled the dynamic occupancy using the program R package 'unmarked' with the function 'colext' (Fiske et al. 2011).

Based on our a priori hypothesis, ψ, γ and ε were modeled as a response to nearness to previously invaded areas, rainfall, water deficit, temperature of winters, forest edge density, greening and browning of forests, fire, urbanization, timber extraction, and livestock grazing. While estimating the ψ, γ was kept constant as a function of nearness to previously invaded sites, ε and P was kept as a function of year. While estimating the γ, ψ was kept constant as a function of single best covariate explaining the presence of species, ε was kept null and P was kept as a function of year. While modeling the probability of extinction ε, ψ was kept constant as a function of single best covariate explaining the presence of species, γ was kept constant as a function of nearness to historically invaded sites, and p was kept as a function of year. Model comparisons were made on the basis of AICc scores. Model with least AIC was considered to be the best model (Johnson & Omland 2004) that explained occurrence of Lantana. When models differed by <5 AIC, I used model average estimates weighted by AIC weights to incorporate model uncertainty in parameter estimates (MacKenzie et al. 2017). Subsequently by using the best model for ψ, γ and ε, I chose the best dynamic models reflecting these modeled parameters and the effect of covariates on them. I interpreted the strength of relationships between covariates and ψt, εt, γt and Pt based on the 95% confidence intervals (CI) of model-averaged back transformed coefficients and the direction of relationships. I used the 'predict' function in the 'unmarked' package to map the predictions of all model parameters (ψt, εt, γt and Pt). Based on the dynamic occupancy model of 2006, 2010 and 2014, I predicted the occupancy of invasive plants for the year 2018, using the contemporary covariates. Subsequently, I used the invasive plants presence from the sampling of 2018 to validate our projections, using True Skill Statistics, which differentiates the accuracy of classifying presence and absence.

Result

Naive occupancy of different invasive plants ranged from 0.63 to 0.76 and had an insignificant change across the sampling years (Appendix 4). The difference in naive occupancy, and occupancy modeled through site covariates differed significantly (5 -13%) for few species (*Ageratina adenophora*, *Ageratum conyzoides*, *Hyptis suaveolens*, *Mimosa diplotricha* and *Xanthium strumarium*) while only a little (0.7 - 4%) for other species (*Chromolaena odorata*, *Lantana camara*, *Mikania micrantha*, *Parthenium hysterophorus*, *Prosopis juliflora* and *Senna tora*). An example of difference in naive and modeled occupancy for *Lantana camara* in dry and moist forests is shown in the figure 20. The detection probability (P) differed across species, but was more or less similar for a species across the sampling years. The average P for every species across the sampling period across the forest type was: 0.76 for *Ageratina adenophora*, 0.74 for *Ageratum conyzoides*, 0.88 for *Chromolaena odorata*, 0.69 for *Hyptis suaveolens*, 0.93 for *Lantana camara*, 0.76 for *Mikania micrantha*, 0.80 for *Mimosa diplotricha*, 0.63 for *Parthenium hysterophorus*, 0.89 for *Prosopis juliflora*, 0.84 for *Senna tora* and 0.70 for *Xanthium strumarium*. An example of detection probability of *Lantana camara* in dry and moist forests across the sampling period in provided in figure 21.

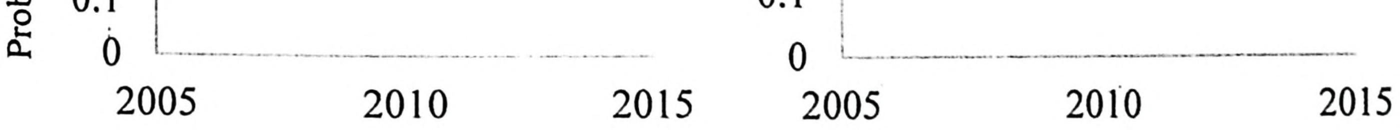


Figure 22 Probability of naïve (orange) and modelled (blue) occupancy of *Lantana camara* in the dry forests (left) and moist forests (right) of India, across the sampling years

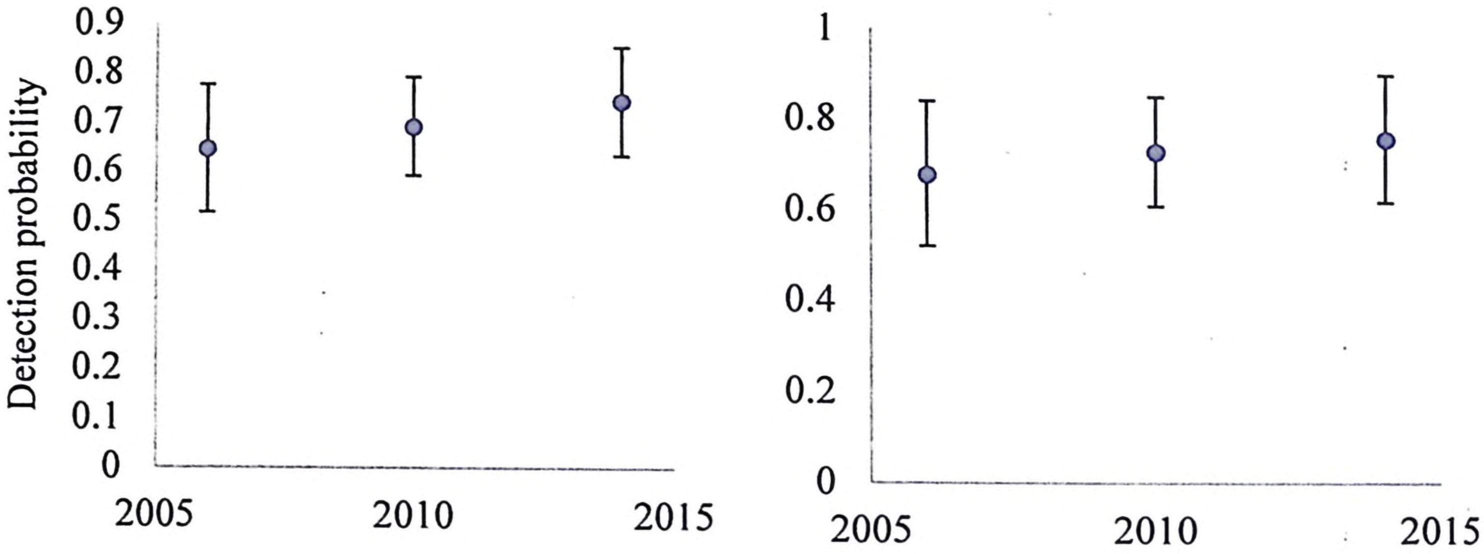


Figure 23 Detection probability of *Lantana camara* in dry forests (left) and moist forests (right) of India, across the sampling years

Dynamic occupancy models revealed that the spread of different invasive plants was explained by different site covariates. An example of AIC based model selection for estimating the ψ, γ, ε, and dynamic occupancy for *Lantana camara* is shown in the table10, 11, 12 and 13. For all the invasive plants in consideration, nearness to previously invaded sites was the single best predictor that explained the colonization probability of a grid, in both the forest types (dry and moist forests). There were few species for which when γ was modeled alone, it showed a combination of covariates explaining the γ. But it was dropped during parsimonious selection of site covariates for overall dynamic occupancy model for that species. These species and their γ covariates were: *Mikania micrantha* (nearness to previously invaded site and distance from fire), *Mimosa diplotricha* (nearness to previously invaded site and water deficit), *Ageratum conyzoides* (nearness to previously invaded site and distance from fire) and *Senna tora* (nearness to previously invaded site and livestock grazing). The probability of colonization decreased after 10 km for *Ageratina adenophora*, 5 km for *Ageratum conyzoides*, 12 km for *Chromolaena odorata*, 4 km for *Hyptis suaveolens*, 15 km for *Lantana camara*, 8 km for *Mikania micrantha*, 4 km for *Mimosa diplotricha*, 7 km for *Parthenium hysterophorus*, 18 km for *Prosopis juliflora*, 22 km for *Senna tora* and 5 km for *Xanthium strumarium*. The best model explaining the extinction of all species across both the forest types was the null model. The relationship between the modelled occupancy and average density across the plots within the site was explored. It revealed a significant positive relationship in occupancy and density, thereby suggesting the utility of occupancy output as density surface (example: Box 1).

Table 10 AIC based model selection based for covariates explaining the occupancy probability of *Lantana camara* in dry forests of India

Model	AIC	Δ AIC	No. para
Climate			
ψ (Annual Precipitation (AP)). γ (IS) ε (.) P (year)	79103	499	5
ψ (Mean temperature of coldest quarter (TC)). γ (IS) ε (.) P (year)	79139	535	5
ψ (AP+TC). γ (IS) ε (.) P (year)	78836	232	6
Water and invasion pressure			
ψ (Water deficit (WD)). γ (IS) ε (.) P (year)	79282	678	5
ψ (IS). γ (IS) ε (.) P (year)	79166	562	5
ψ (WD+IS). γ (IS) ε (.) P (year)	78964	360	6
Human footprint			
ψ (Nightlight (NL)). γ (IS) ε (.) P (year)	79088	484	5
ψ (Timber extraction (TE)). γ (IS) ε (.) P (year)	79402	798	5
ψ (Livestock seen (LS)). γ (IS) ε (.) P (year)	79284	680	5
ψ (Forest edge (FE)). γ (IS) ε (.) P (year)	79377	773	5
ψ (Forest browning (FB)). γ (IS) ε (.) P (year)	79077	473	5
ψ (Fire frequency (FF)). γ (IS) ε (.) P (year)	79182	578	5
ψ (NL+TE+LS+FE+FB+FF). γ (IS) ε (.) P (year)	79411	807	10
ψ (NL+FB+FF). γ (IS) ε (.) P (year)	79203	599	7
Combination			
ψ (AP+TC+NL+FB+FF+IS+WD). γ (IS) ε (.) P (year)	78812	208	11
ψ (AP+TC+NL+FB+FF+IS). γ (IS) ε (.) P (year)	78604	0	10

Table 11 AIC based model selection based for covariates explaining the colonization probability of *Lantana camara* in dry forests of India

Model	AIC	Δ AIC	No. parameters
ψ (FB). γ (Invaded sites (IS)) ε (.) P (year)	86451	0	5
ψ (FB). γ (Livestock seen (LS)) ε (.) P (year)	86621	170	5
ψ (FB). γ (Nightlight (NL)) ε (.) P (year)	86653	202	5
ψ (FB). γ (Timber extraction (TE)) ε (.) P (year)	86700	249	5
ψ (FB). γ (NL+TE+LS+IS) ε (.) P (year)	86742	291	8
ψ (FB). γ (FB) ε (.) P (year)	86754	303	5
ψ (FB). γ (Fire frequency (FF)) ε (.) P (year)	86826	375	5
ψ (FB). γ (WD+NL+TE+LS+FE+FB+FF+IS) ε (.) P (year)	86942	491	12
ψ (FB). γ (Forest edge (FE)) ε (.) P (year)	86992	541	5
ψ (FB). γ (Water deficit (WD)) ε (.) P (year)	87008	557	5
ψ (Forest browning (FB)). γ (.) ε (.) P (year)	87141	690	5

Table 12 AIC based model selection based for covariates explaining the extinction probability of *Lantana camara* in dry forests of India

Model	AIC	Δ AIC	No. para
ψ (Forest browning (FB)). γ (Invaded sites (IS)) ε (.) P (year)	42156	0	5
ψ (FB). γ (IS) ε (Water deficit (WD)) P (year)	42551	395	5
ψ (FB). γ (IS) ε (Fire frequency (FF)) P (year)	42653	497	5
ψ (FB). γ (IS) ε (Timber extraction (TE)) P (year)	42804	648	5
ψ (FB). γ (IS) ε (WD+FF) P (year)	42821	665	6
ψ (FB). γ (IS) ε (Livestock grazing (LS)) P (year)	42912	756	5
ψ (FB). γ (IS) ε (WD+FF+TE+LS) P (year)	43110	954	8

Table 13 AIC based model selection based for covariates explaining the dynamic occupancy of *Lantana camara* in dry forests of India

Model	**AIC**	**Δ AIC**	**No. para**
ψ (AP+TC+NL+FB+FF). γ (IS) ε (.) P (year)	**56201**	**0**	**9**
ψ (AP+TC+NL+FB+FF). γ (IS+LS) ε (.) P (year)	56338	**137**	10
ψ (AP+TC+NL+FB+FF+IS+WD). γ (IS) ε (.) P (year)	56421	**220**	11
ψ (AP+TC+NL+FB+FF+IS). γ (IS+LS) ε (.) P (year)	56540	**339**	11
ψ (AP+TC+NL+FB+FF+IS). γ (IS) ε (WD) P (year)	56589	**388**	10
ψ (AP+TC+NL+FB+FF+IS). γ (IS+LS) ε (WD) P (year)	56616	**415**	11
ψ (AP+TC+NL+FB+FF+IS). γ (IS) ε (.) P (year)	56671	**470**	10
ψ (AP+TC+NL+FB+FF+IS+WD). γ (IS) ε (WD) P (year)	56769	**568**	11
ψ (FB). γ (IS) ε (.) P (year)	56918	**717**	5
ψ (FB). γ (LS) ε (.) P (year)	57201	**1000**	5
ψ (FB). γ (IS) ε (.) P (year)	57350	**1149**	5
ψ (FB). γ (IS) ε (WD) P (year)	57495	**1294**	5

The occupancy estimated per grid and the site covariates explaining it was different per species in both forest types. The beta coefficients of each covariate for every species in their respective forest type is provided in from table 14 to table 24. For both the forest types, and for all species, urbanization, timber extraction, forest edge density, and higher temperature of winters increased the occupancy of invasive plants. The relation between these invasive plants and other covariates varied for both the forest types. When the standardized beta coefficients of species-covariate relationship were compared between moist and dry forests, I observed the relationship to be on an average opposite (figure 22). While higher rainfall decreased invasive plant occupancy in moist forest, it increased the occupancy in dry forest. Water deficit increased the invasive plant occupancy in moist forest, it decreased the occupancy in dry forest. While gradual increase in vegetation cover decreased invasive plant occupancy in moist forest, it increased the occupancy in dry forest. While fire and livestock grazing increased the invasive plant occupancy in moist forest, it decreased the occupancy in dry forest.

Table 14 Covariates explaining the dynamic occupancy of *Ageratina adenophora*

Parameter	Covariates	Moist forest Coefficient estimate
ψ	Constant (Intercept)	0.51 (±0.19)
	Annual precipitation	-0.09 (±0.02)
	Mean temperature of coldest quarter	0.46 (±0.01)
	Nightlight	0.32 (±0.07)
	Forest edge density	0.07 (±0.01)
	Fire frequency	0.05 (±0.01)
	Water deficit	0.17 (±0.08)
γ	2010	0.19 (±0.10)
	2014	0.22 (±0.06)
	Distance from invaded sites	-0.61 (±0.01)
ε	2010	-0.07 (±0.05)
	2014	-0.03 (±0.06)
p	2006	0.66 (±0.04)
	2010	0.70 (±0.12)
	2014	0.76 (±0.16)

Table 15 Covariates explaining the dynamic occupancy of *Ageratum conyzoides*

Parameter	Covariates	Moist forest Coefficient estimate	Dry forest Coefficient estimate
ψ	Constant (Intercept)	0.36 (±0.10)	0.19 (±0.08)
	Annual precipitation	-0.11 (±0.03)	0.42 (±0.04)
	Mean temperature of coldest quarter	0.19 (±0.03)	0.14 (±0.03)
	Nightlight	0.30 (±0.09)	0.22 (±0.03)
	Forest browning	0.25 (±0.02)	-0.08 (±0.01)
	Fire frequency	0.03 (±0.01)	-0.10 (±0.04)
	Livestock grazing	0.33 (±0.07)	-0.06 (±0.01)
γ	2010	0.36 (±0.07)	0.49 (±0.02)

	2014	0.48 (±0.18)	0.63 (±0.22)
	Distance from invaded sites	-0.40 (±0.04)	-0.43 (±0.08)
ε	2010	-0.18 (±0.12)	-0.37 (±0.20)
	2014	-0.04 (±0.08)	-0.09 (±0.06)
p	2006	0.78 (±0.10)	0.70 (±0.03)
	2010	0.81 (±0.03)	0.73 (±0.02)
	2014	0.79 (±0.04)	0.81 (±0.05)

Table 16 Covariates explaining the dynamic occupancy of *Chromolaena odorata*

Parameter	**Covariates**	**Moist forest Coefficient estimate**	**Dry forest Coefficient estimate**
ψ	Constant (Intercept)	0.41 (±0.11)	0.53 (±0.18)
	Annual precipitation	-0.63 (±0.04)	0.58 (±0.05)
	Mean temperature of coldest quarter	0.16 (±0.01)	0.07 (±0.02)
	water deficit	0.14 (±0.03)	-0.08 (±0.02)
	Forest browning	0.07 (±0.01)	-0.18 (±0.02)
	Timber extraction	0.02 (±0.01)	0.06 (±0.01)
	Livestock grazing	0.11 (±0.02)	-0.04 (±0.03)
γ	2010	0.32 (±0.04)	0.58 (±0.09)
	2014	0.46 (±0.07)	0.69 (±0.11)
	Distance from invaded sites	-0.28 (±0.01)	-0.70 (±0.05)
ε	2010	-0.08 (±0.04)	-0.12 (±0.01)
	2014	-0.06 (±0.03)	-0.08 (±0.04)
p	2006	0.66 (±0.03)	0.73 (±0.02)
	2010	0.78 (±0.05)	0.70 (±0.01)
	2014	0.84 (±0.02)	0.85 (±0.07)

Table 17 Covariates explaining the dynamic occupancy of *Hyptis suaveolens*

Parameter	**Covariates**	**Moist forest Coefficient estimate**	**Dry forest Coefficient estimate**
ψ	Constant (Intercept)	0.12 (±0.05)	0.34 (±0.13)

	Annual precipitation	-0.64 (±0.03)	0.58 (±0.04)
	Forest edge density	0.40 (±0.02)	0.14 (±0.01)
	Nightlight	0.36 (±0.01)	0.18 (±0.02)
	Forest browning	0.03 (±0.02)	-0.08 (±0.02)
	Timber extraction	0.08 (±0.01)	0.12 (±0.02)
	Water deficit	0.27 (±0.06)	-0.04 (±0.01)
γ	2010	0.36 (±0.05)	0.34 (±0.03)
	2014	0.40 (±0.1)	0.36 (±0.04)
	Distance from invaded sites	-0.73 (±0.04)	-0.86 (±0.08)
ε	2010	-0.06 (±0.05)	-0.08 (±0.05)
	2014	-0.02(±0.03)	-0.04 (±0.02)
p	2006	0.80 (±0.03)	0.83 (±0.02)
	2010	0.78 (±0.04)	0.90 (±0.06)
	2014	0.82 (±0.07)	0.93 (±0.08)

Table 18 Covariates explaining the dynamic occupancy of *Lantana camara*

Parameter	**Covariates**	**Moist forest Coefficient estimate**	**Dry forest Coefficient estimate**
ψ	Constant (Intercept)	0.44 (±0.18)	0.79 (±0.13)
	Annual precipitation	-0.136 (±0.032)	0.321 (±0.06)
	Mean temperature of coldest quarter	0.26 (±0.019)	0.204 (±0.02)
	Nightlight	0.287 (±0.08)	0.297 (±0.04)
	Forest browning	-0.016 (±0.002)	0.032 (±0.02)
	Fire frequency	0.041 (±0.01)	-0.097 (±0.03)
γ	2010	0.51 (±0.07)	0.54 (±0.13)
	2014	0.63 (±0.14)	0.74 (±0.17)
	Distance from invaded sites	-0.36 (±0.071)	-0.3 (±0.02)
ε	2010	-0.08 (±0.05)	-0.06 (±0.02)
	2014	-0.03 (±0.08)	-0.07 (±0.05)
p	2006	0.643 (±0.04)	0.683 (±0.05)
	2010	0.67 (±0.03)	0.701 (±0.03)
	2014	0.694 (±0.05)	0.722 (±0.02)

Table 19 Covariates explaining the dynamic occupancy of *Mimosa diplotricha*

Parameter	**Covariates**	**Moist forest Coefficient estimate**
ψ	Constant (Intercept)	0.27 (±0.13)
	Annual precipitation	-0.62 (±0.03)
	Mean temperature of coldest quarter	0.31 (±0.02)
	Nightlight	0.15 (±0.01)
	Forest edge density	0.23 (±0.01)
	Fire frequency	0.06 (±0.03)
	Water deficit	-0.07 (±0.08)
γ	2010	0.23 (±0.14)
	2014	0.46 (±0.21)
	Distance from invaded sites	-0.74 (±0.02)
ε	2010	-0.28 (±0.09)
	2014	-0.12 (±0.15)
p	2006	0.69 (±0.02)
	2010	0.73 (±0.01)
	2014	0.81 (±0.02)

Table 20 Covariates explaining the dynamic occupancy of *Mikania micrantha*

Parameter	**Covariates**	**Moist forest Coefficient estimate**
ψ	Constant (Intercept)	0.45 (±0.18)
	Annual precipitation	0.401 (±0.04)
	Mean temperature of coldest quarter	0.294 (±0.09)
	Water deficit	0.218 (±0.07)
	Nightlight	0.146 (±0.02)
	Forest edge density	0.09 (±0.01)
γ	2010	0.14 (±0.07)
	2014	0.23 (±0.12)
	Distance from invaded sites	0.398 (±0.06)
	Fire frequency	0.156 (±0.03)
ε	2010	-0.11 (±0.04)

	2014	-0.1 (±0.09)
p	2006	0.63 (±0.07)
	2010	0.68 (±0.09)
	2014	0.7 (±0.1)

Table 21 Covariates explaining the dynamic occupancy of *Parthenium hysterophorus*

Parameter	**Covariates**	**Moist forest Coefficient estimate**	**Dry forest Coefficient estimate**
ψ	Constant (Intercept)	0.36 (±0.16)	0.42 (±0.2)
	Annual precipitation	-0.42 (±0.02)	0.35 (±0.03)
	Mean temperature of coldest quarter	0.13 (±0.01)	0.18 (±0.02)
	Forest edge density	0.23 (±0.01)	0.37 (±0.01)
	Nightlight	0.21 (±0.02)	0.31 (±0.02)
	Livestock grazing	0.13 (±0.01)	-0.04 (±0.03)
	Fire	0.09 (±0.01)	-0.14 (±0.01)
	Water deficit	0.17 (±0.04)	-0.10 (±0.03)
γ	2010	0.43 (±0.06)	0.59 (±0.03)
	2014	0.58 (±0.24)	0.64 (±0.21)
	Distance from invaded sites	-0.47 (±0.07)	-0.65 (±0.04)
ε	2010	-0.13 (±0.1)	-0.11 (±0.12)
	2014	-0.05 (±0.03)	-0.07 (±0.04)
p	2006	0.69 (±0.03)	0.84 (±0.01)
	2010	0.75 (±0.02)	0.73 (±0.02)
	2014	0.83 (±0.01)	0.79 (±0.01)

Table 22 Covariates explaining the dynamic occupancy of *Prosopis juliflora*

Parameter	**Covariates**	**Dry forest Coefficient estimate**
ψ	Constant (Intercept)	0.72 (±0.27)
	Annual precipitation	0.39 (±0.02)
	Mean temperature of coldest quarter	0.21 (±0.01)
	Nightlight	0.27 (±0.02)
	Forest browning	0.17 (±0.01)
	Livestock grazing	-0.07 (±0.03)

	Fire	-0.04 (±0.01)
	Water deficit	-0.12 (±0.03)
γ	2010	0.75 (±0.24)
	2014	0.79 (±0.09)
	Distance from invaded sites	-0.79 (±0.02)
ε	2010	-0.04 (±0.06)
	2014	-0.06 (±0.05)
p	2006	0.86 (±0.01)
	2010	0.93 (±0.01)
	2014	0.95 (±0.01)

Table 23 Covariates explaining the dynamic occupancy of *Senna tora*

Parameter	Covariates	Moist forest Coefficient estimate	Dry forest Coefficient estimate
ψ	Constant (Intercept)	-0.71 (±0.03)	-0.68 (±0.01)
	Annual precipitation	-0.39 (±0.01)	0.51 (±0.02)
	Mean temperature of coldest quarter	0.16 (±0.02)	0.21 (±0.01)
	Forest edge density	0.15 (±0.04)	0.42 (±0.03)
	Nightlight	0.20 (±0.02)	0.37 (±0.02)
	Livestock grazing	0.42 (±0.02)	0.09 (±0.06)
	Fire	0.05 (±0.01)	-0.6 (±0.03)
γ	2010	0.64 (±0.11)	0.54 (±0.17)
	2014	0.82 (±0.09)	0.66 (±0.14)
	Distance from invaded sites	-0.45 (±0.02)	-0.77 (±0.03)
ε	2010	-0.55 (±0.19)	-0.62 (±0.11)
	2014	-0.24 (±0.11)	-0.19 (±0.03)
p	2006	0.79 (±0.01)	0.83 (±0.01)
	2010	0.87 (±0.03)	0.88 (±0.02)
	2014	0.91 (±0.04)	0.90 (±0.02)

Table 24 Covariates explaining the dynamic occupancy of *Xanthium strumarium*

Parameter	Covariates	Moist forest Coefficient estimate	Dry forest Coefficient estimate
ψ	Constant (Intercept)	-0.57 (±0.04)	-0.61 (±0.05)
	Annual precipitation	-0.41 (±0.02)	0.32 (±0.02)
	Mean temperature of coldest quarter	0.11 (±0.03)	0.14 (±0.05)
	Forest edge density	0.19 (±0.07)	0.16 (±0.03)
	Nightlight	0.09 (±0.01)	0.13 (±0.03)
	Water deficit	-0.12 (±0.07)	-0.09 (±0.04)
	Fire	0.04 (±0.01)	-0.06 (±0.01)
γ	2010	0.47 (±0.02)	0.49 (±0.01)
	2014	0.56 (±0.06)	0.63 (±0.13)
	Distance from invaded sites	-0.39 (±0.02)	-0.67 (±0.02)
ε	2010	-0.57 (±0.04)	-0.60 (±0.02)
	2014	-0.33 (±0.07)	-0.28 (±0.13)
p	2006	0.70 (±0.01)	0.82 (±0.01)
	2010	0.83 (±0.02)	0.84 (±0.01)
	2014	0.79 (±0.03)	0.85 (±0.02)

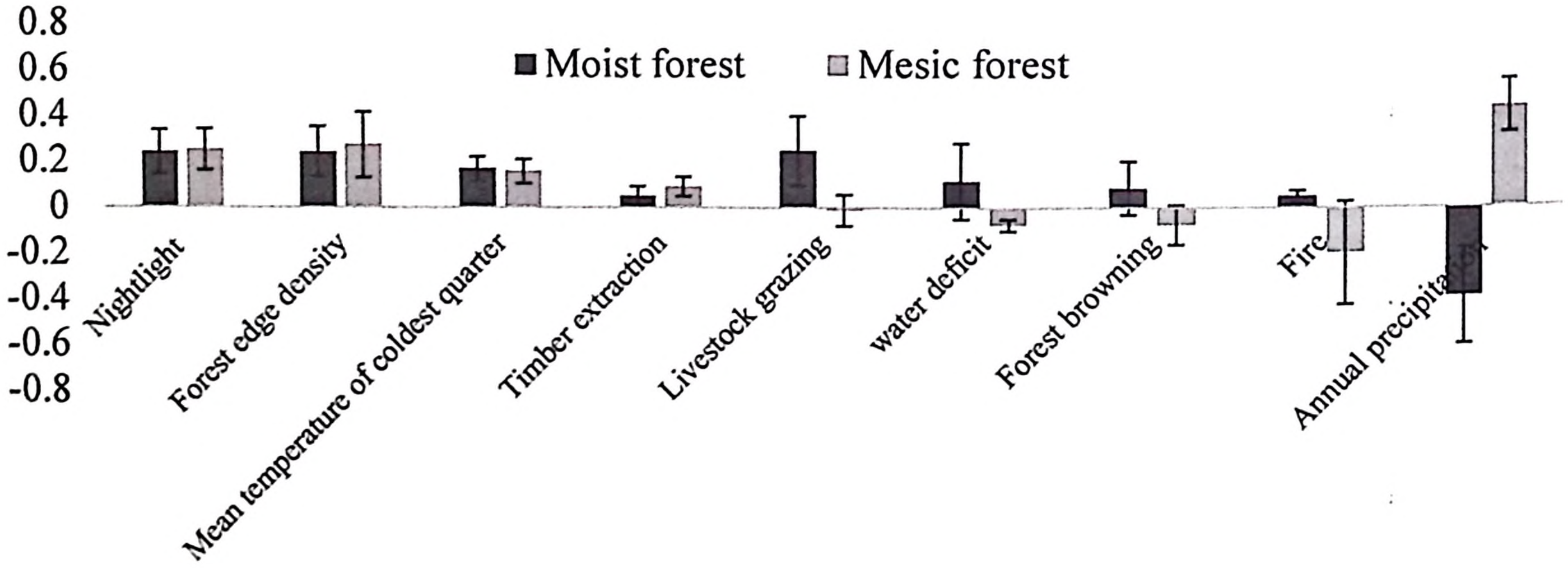
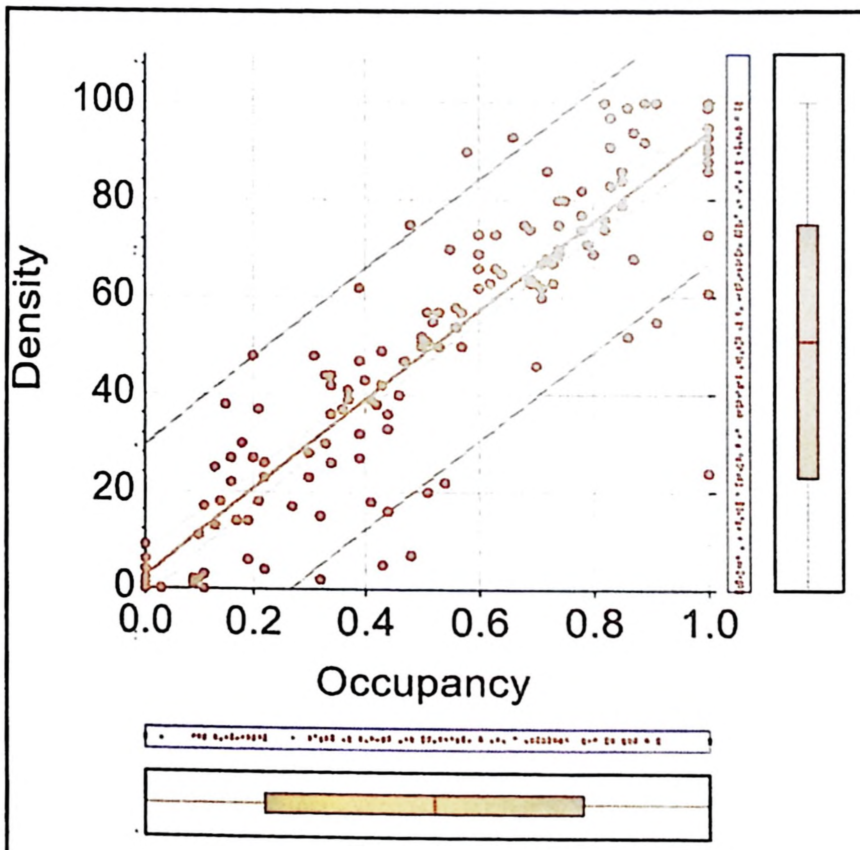


Figure 24 Standardized beta coefficients (SE) of different site covariates explaining the average occupancy across species in the moist and dry forests of India.

When the observed trend from 2006-2014 was projected to 2018, I found that the projected and observed occupancy were significantly similar. The projected model could on an average 92 (±4) % and 78 (±11) % accurately classify presences and absences, respectively. The average rate of invasion per year, after correcting for detection and site covariates across forest types for different invasive plants was: 440 (±62) km^2 for *Ageratina adenophora*, 586 (±106) km^2 for *Ageratum conyzoides*, 735 (±214) km^2 for *Chromolaena odorata*, 242 (±78) km^2 for *Hyptis suaveolens*, 890 (±369) km^2 for *Lantana camara*, 954 (±278) km^2 for Mikania *micrantha*, 188 (±46) km^2 for *Mimosa diplotricha*, 153 (±102) km^2 for *Parthenium hysterophorus*, 761 (±337) km^2 for *Prosopis juliflora*, 310 (±152) km^2 for *Senna tora* and 220 (±119) km^2 *Xanthium strumarium*.



Box 1: Occupancy and abundance relationship: Scatter plot and linear regression between occupancy probability of a 25 km^2 grid (x-axis) and abundance (y-axis) in percent cover of *Lantana camara* in 10m diameter plots average at 25 km^2 grids. The data was selected from 24 Tiger Reserves where sampling was conducted and the species was detected.

Summary statistics:
Slope = 2.484 (± 2.074)
Intercept = 91.429 (± 3.416)
$P < 0.01$
R^2 value: 0.82

Discussion

As shown in chapter 3, the rate of spread of invasive plants was overwhelmingly high (average spread across species was 808 (±442) km2/year). After correcting for detection and site covariates, it was dropped to 533 (±291) km2/year. Currently, 79% of the total forested areas are invaded by at least one of the high concern invasive plants. With the current rate of spread, 0.1 (±0.05) % of the uninvaded forest area in India is being invaded every year by one of the high concern invasive plants. Overall occupancy of invasive plants was observed to be higher in the dry forests of central India, followed by the moist forests of Western Ghats. Least invaded areas were observed in the Northeastern hills. But this could also be due to relatively less sampling.

Results suggested that invasive plants were spreading around existing invaded areas, irrespective of the forest characters, water deficit, human disturbance or climatic parameters. This represents that invasive plants might take advantage of unutilized resources availed due to human disturbance or global changes, but later spread independent of any particular environmental conditions. If a non-invaded site is close to many other invaded sites, its likelihood of getting invaded is higher by most of the invasive plants. On the contrary, extinction of the invasive plant was neither explained by any environmental covariate. This can be explained by two facts: the number of grids in which invasive plants have recorded extinction are miniscule; and during field sampling, most of the extinctions were observed due to managerial control that was not considered in the model. Managerial control operates on different priority at varying temporal scale, to quantify it at each grid was not possible and was hence not recorded.

The occupancy was positively related with the degraded drier areas in moist forests and productive water rich areas in dry forests. In India, moist forest areas are being fragmented by different developmental activities and global changes (Ravindranath et al. 2012), while dry forests are being irrigated and greened by plantations and agriculture (Ratnam et al. 2016). Results suggested that these are favorable conditions for the alarming rate of spread of invasive plants. It also indicates that while native plants in moist forests are vulnerable to drier environments and plants in dry forests are vulnerable to moist environment, invasive plants can be plastic to take advantage of these changes and invaded in both the forest types by altering their responses. Chapter 4 demonstrated that invasive plants change their response to their niche axis across the biogeographic realm; here I show that the species response also change at regional ecological realms.

Parameters like heavy rainfall in the drier areas, and less rainfall in the moist areas, higher winter temperature, browning of forests and urban expansion are major indicators of global climatic changes. Results suggests that invasive plants take advantage of these changes irrespective of in which forest type they are present. Local scale anthropogenic pressures however have different responses to different species in different settings. While timber extraction increased the occupancy of invasive plants across the sampling area, livestock grazing and fire increased invasive plants in moist forests only. Urbanization and forest fragmentation due to linear infrastructure, on the contrary, increased invasive plant occupancy across the tropical Indian forest system. Thus, in the wake of the ongoing global climatic changes and regional forest depletion brought by developmental activities, more and more of the India's native forest is vulnerable to the invasion of these plants. It is essential to safeguard the uninvaded forests from future invasions. Our models suggest that uninvaded forests that are close to invaded sites are more vulnerable. Hence, an active monitoring of habitat is essential, particularly in the protected areas, so that any invasion is controlled in initial stage. It is crucial to understand that with the ongoing changes, which patches of the forests will be more vulnerable due to the spread of invasive plants. I address this in the next chapter.

Effect of proximity to invaded patch and the complexity of invasive plant management:

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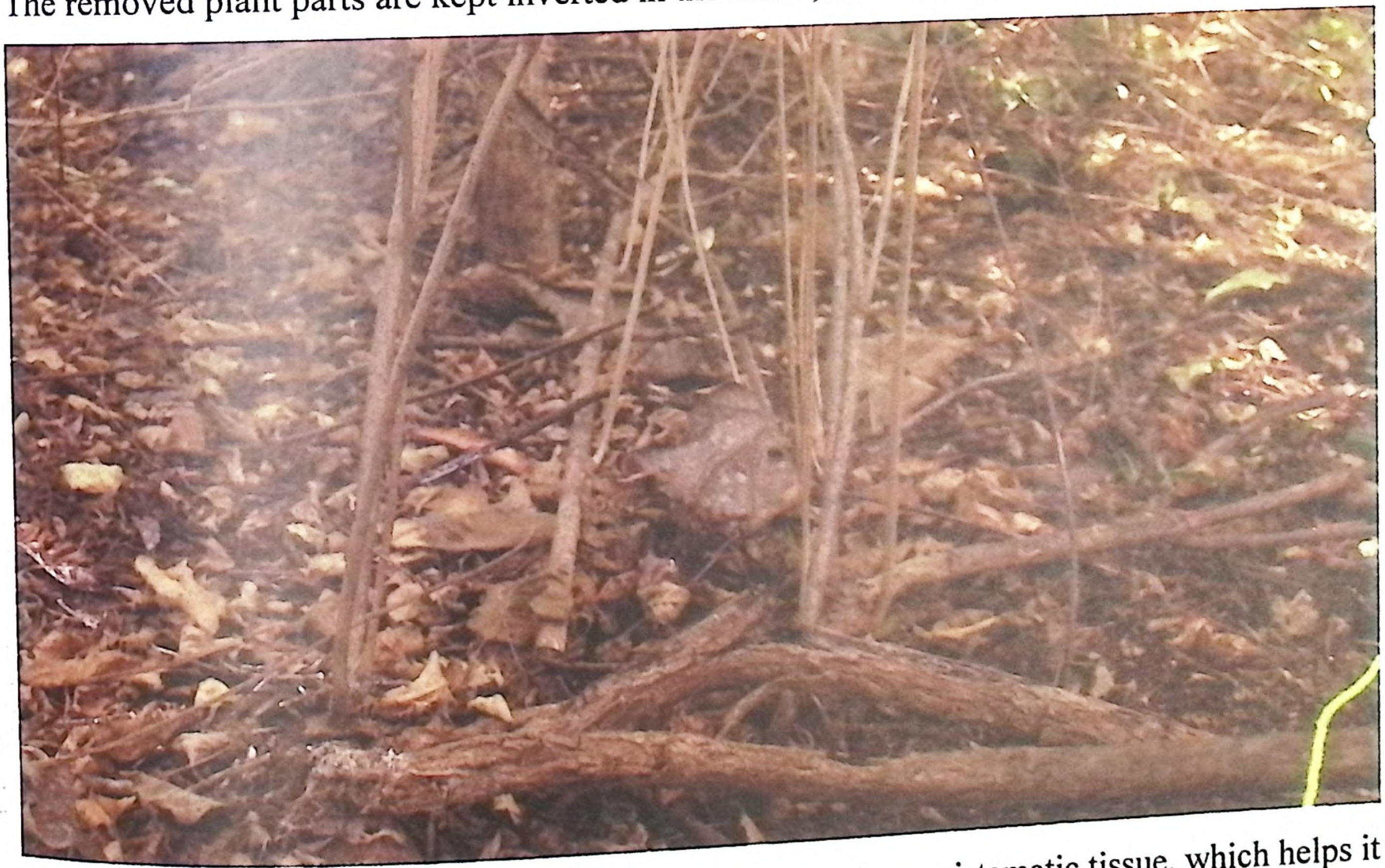
In the open deciduous forests across India, where *Lantana camara* occurs in high densities, managers often imply root-stalk-cut method to effectively remove this plant from the forests. The removed plant parts are kept inverted in the forest, so that they do not grow again.



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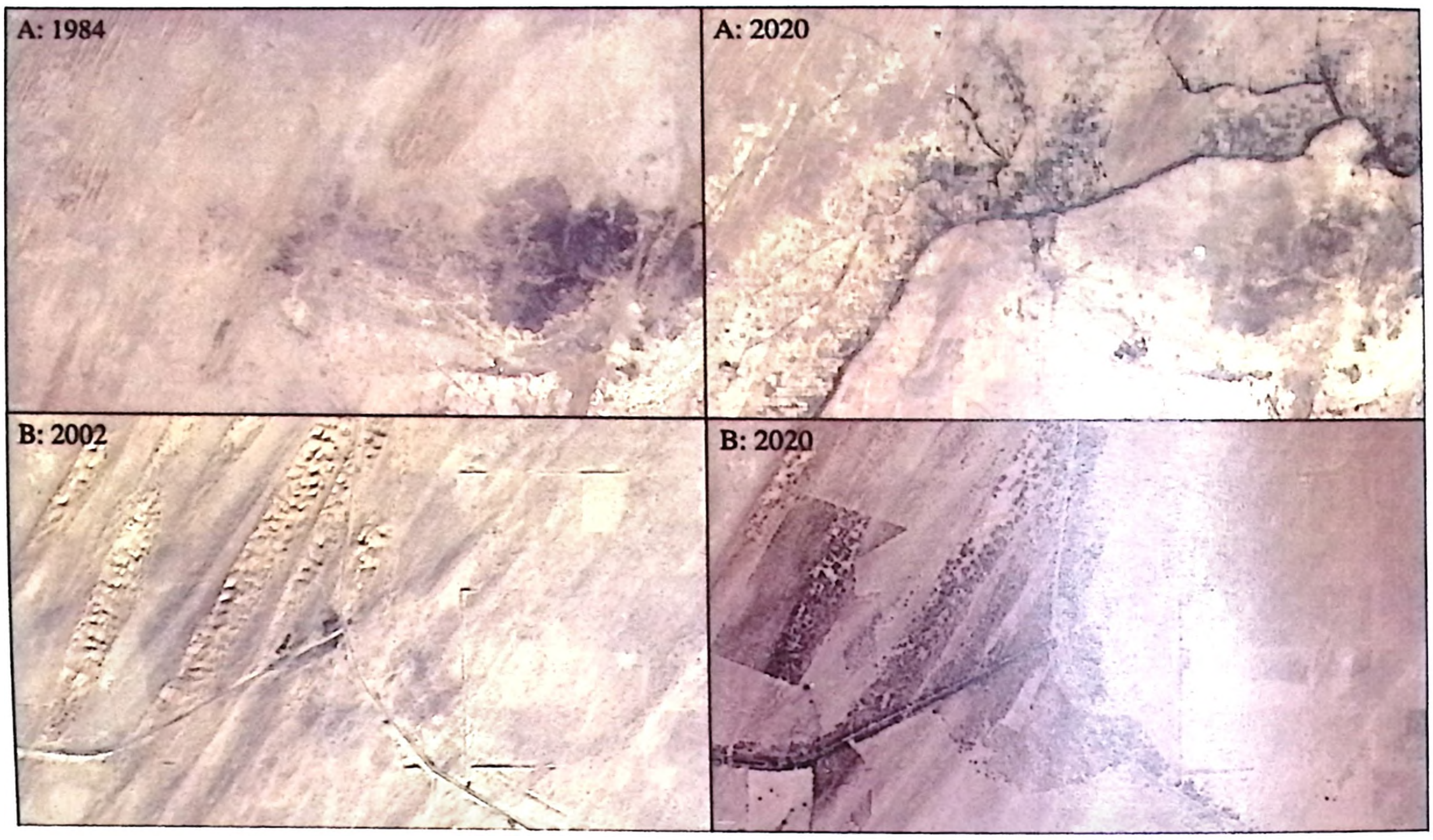
But, the stem of *Lantana camara* is known to be coated by meristematic tissue, which helps it regenerate from any part of the stem on contact with ground and water. As a result, the plant reinvades the patch as well as disperses around the site. Similar regeneration is observed in *Ageratina Adenophora, Chromolaena odorata, Mikania micrantha* and *Mimosa diplotrica*.

Effect of altering moisture regime in dry ecosystems:



Google Earth images showing rapid changes in the Thar desert of India. A) arid areas of 1980s are now converted to crop farms surrounded by invasive *Prosopis juliflora*, following the enhanced irrigation schemes B) Sand dunes where agriculture couldn't efficiently last were converted to woody plantations, which is also now invaded by *Prosopis juliflora*

Grasslands along the Ganga river and its tributaries are invaded by *Prosopis juliflora* and *Xanthium strumarium*, following reduced flow in the low stream areas of dams and barrages.

CHAPTER 7: EFFECT OF FUTURE SCENARIOS ON INVASIVE PLANTS

Part of the chapter was published as a peer-reviewed publication: Mungi NA, Coops NC, Ramesh K, Rawat GS. (2018) How global climate change and regional disturbance can expand the invasion risk? Case study of Lantana camara invasion in the Himalaya. Biological Invasions 20(7):1849-1863.https://doi.org/10.1007/s10530-018-1666-7

"All models are wrong, but some are useful" - George E.P. Box, 1978

Introduction:

Invasive species, climate change and anthropogenic disturbances are interactive and pervasive challenge to the world's biodiversity (O'Neill et al. 2018). These challenges are more severe in the tropics, where the rates of demographic increase and socio-economic changes are declining the biodiversity (Barlow et al. 2018). The resultant decline is believed to hamper the associated services and global human-welfare; with tropical developing societies being the most vulnerable (Barlow et al. 2018). For an example, deforestation in south and southeast Asia has receded the Asian monsoon (Devaraju et al. 2016). Deforestation and weakening monsoon is known to facilitate invasive species, which in turn reduces future forest regeneration that hampers future monsoon; as well as threaten the food security in the region (Lawrence & Vandecar 2015). This interactive effect can have severe consequences on the native ecology and economy of the region, particularly in the wake of rapid developmental activities and ongoing climatic changes, which is degrading the native forest ecosystem. While the effect of deforestation and climate change is increasingly addressed (Shukla et al. 1990), invasive species are prone to be considered in isolation from these stressors; thereby creating a void in understanding how the imminent global and regional changes will influence the invasive species.

Future trajectories in India offer a central case of world's climate change scenario. Because here, the world's highest human population will strive for food and water security, increased GDP, energy and technology; and yet hold eight percent of the global biodiversity. Most of these stressors have improved India's economic development in the last 50 years, but only at a cost of loss in its natural ecosystems and rapid biological invasions. However, these stressors are known to globally satiate with decline in the population growth and through developing sustainable strategies that subsequently alters consumption of energy, land and natural resources. These strategies are often the technological revolution, which experience a long friction until widely accepted - also known as 'creative destruction' (Schumpeter 1942). For example, in India, solar power energy is projected to overcome the current coal-based energy demand, and is visible in the latest energy policies of the country. Coal mining is one main reason for increased carbon emission and forest fragmentation in India, which will subsequently decline with increased solar power production. However, the hindrance in developing other similar sustainable strategies mainly rest on the inertia to challenge the traditional productions, insecurities in the investments, and absence of policies and subsidies. As a consequence, there exists alternate futures as a function of the present-day choices driven by democratic policies and environmental awareness. The global initiatives like the Paris agreement, Global Deal for Nature, etc. represent a movement in environmentally sensitive public policies, followed by the 200 signatory countries - including India. The model of sustainable future offered by these initiatives are being testified for effective conservation of earth's natural ecosystems (Thatte et al. 2018). However, the particular case of effects on invasive species is less modelled at a large-scale by considering the regional and global drivers of changes.

Several recent publications modeled the potential influence of changing climate and anthropogenic pressure on invasive species (Liu et al. 2017; Merow et al. 2017; Mungi et al. 2018; Di Febbraro et al. 2019). However, they suffer data limitations on presence of invasive species, or by restricting to only climatic or land-use scenarios. The limitations are further aggravated by the unattended accuracy of future projections and its ecological relevance, sources of primary data on invasive species, climate stations, and uncertainty of the statistical models used. Despite the large information on global biodiversity (e.g. GBIF, eBird), the opportunistic nature of data has hindered its utility in understanding the present species distribution, thereby only adding to the uncertainty of future modeling. The preliminary requirement for overcoming these limitation is accurate understanding on the large-scale present distribution of invasive species, and modeling alternate futures, based on different socio-economic trajectories. The invasive plants assessment conducted by India is one such long-term large-scale monitoring, which is repeated every fourth year, since 2006, to cover more than 181,662 km· of forested areas. It revealed that 90% of the sampled forests are invaded by the high concern invasive plants (Chapter 3). Due to its quintessential spatial coverage across six biogeographic realms, it offers a unique opportunity to understand the present effects of climate and anthropogenic pressures on invasive plants, and subsequently model the future trajectories for same.

In present chapter, I model the distribution of 11 high concern invasive plants in India, as a function of their ecological drivers identified in chapter 5 and 6, and subsequently project their future distribution. To assess the accuracy and errors in future projections, presence data of the year 2010 was used to project their distribution in the year 2018, which was verified with the data collected in 2018. I further built 2 alternate future scenarios based on the socio-economic trajectories of India for 2030, 2040 and 2050 using forward-time, spatially explicit simulations to project the future spread of invasive plants. These future scenarios were set as a product of societal choices and policies on Land Use change to accommodate increased population and its food and water security, energy production, forest management, and global climatic changes. I examine these scenarios by adding the factor of invasive plants management at priority sites, to produce the first national level future projections of invasive species spread based on real-data, to interpret the necessity and magnitude of management interventions needed to refine the existing model of 'sustainable future'.

Method:

I selected the presence data of 11 high concern invasive plants (*Ageratina adenophora, Ageratum conyzoides, Chromolaena odorata, Hyptis suaveolens, Lantana camara, Mikania micrantha, Mimosa diplotricha, Parthenium hysterophorus, Prosopis juliflora, Senna tora* and *Xanthium strumarium*) from two sampling durations (i.e. non-monsoon seasons of 2010 and 2018). The presence was recorded from the forests of six biogeographic zones present in India, which represents the tropical and sub-tropical climate of the Indian subcontinent that has produced diverse forest types in the region. These forests are surrounded by one of the densest developing human populations in the world, which is rapidly modifying these forests for their livelihood dependencies and developmental activities. Hence, there are multiple drivers, which operate at varying scale as identified in chapter 5 and 6. The relevance of these covariates can be found in the method section of chapter 6. These drivers can be classified as land use (human settlement), resources (water availability), forest fragmentation (mining and linear infrastructure), climate (maximum and minimum temperature, annual precipitation and precipitation of the driest quarter) and forest management (plantation and invasive species management). In place of relying on the parsimonious selection of the drivers to make simplistic models, I choose to develop ecologically informed models (Coelho et al. 2018). The relevance and derivation of these drivers for invasive species distribution in present and alternate future scenarios is discussed in detail below.

The two assumptions on which I project the future scenarios of India are population and GDP (figure 23). As it is now known, India will hold world's largest and desist human population by the next decade. While maintaining its GDP based economy, the country and its population has always been dependent on either the natural resources (e.g. timber, freshwater, etc.) or its modifications (e.g. coal energy, irrigation projects, etc.). Considering the population highest, keeping pace with growing energy demand, and meeting food, water and financial security will imminently precede climate and environment policies. Nevertheless, as a result of scientific awareness, environmentally sensitive policies are emerging to build a sustainable future. For example, tree felling in India is banned by law since 1996; world's largest voluntary human settlement was carried in the protected areas of India to create inviolate areas for wildlife; and the Green India mission under the National Action Plan on Climate Change (Ministry of Environment and Forests, 2008) advocates achieving a forest cover of 33% from current 21% forest cover (Forest Survey of India, 2015). While agricultural production and energy requirement is projected to have larger ecological and carbon footprint till 2030, the recent technological advances are projected to provide alternatives for minimizing the environmental footprint of these drivers. For an example, of the total (net) of 17.6 gigawatts power generation capacity in 2018, a record percentage (74%) was based on renewable energy technologies - primarily solar power. Thus, there exist multiple trajectories, through which India's future could sustain its developmental agenda, while adhering to its ecological imperatives.

The uncertainties in socio-economic choices produces multiple future scenarios, where each trajectory to future is a function of the democratic choices by the country's population at different times. Any smallest of the change in the trajectory, at any given time and space, can lead to an alternate future scenario; thereby, creating a chaotic model of alternate futures. However, in the present study I do not intend to model these trajectories, but understand the consequences of following the 'business-as-usual' model or adhering to the alternatives provided by currently advocated 'sustainable future' model. For building these two alternate future scenarios, I first assess the trend in the drivers of invasive plants in the past two decades (2000-2018). I model this trend as a function of population, food and water security, energy production and GDP growth. Based on these drivers I further extrapolate the future trends (2020, 2030, 2040, and 2050) assuming they remains the same under the 'business-as-usual' model. For the 'sustainable future' model, I rely on the projections provided by the Global Deal for Nature (Dinerstein et al. 2019), The world in 2050, World Economic Forum, and the *Niti Aayog* (Government of India, 2017). I model each covariate under these two alternate future scenario, as provided further (figure 23).

Land Use change:

The imminent change following the population growth is increased land under human settlement and increased urban migration. It is important to identify the rate at which population is sprawling the settlement and urbanizing the existing centres. To do so, I used derivative of nightlight and population density to develop a layer of human settlement. For urban or peri-urban context, I used nightlight; and for rural landscape, which is not completely electrified in India, I used population density data. Following the known relationship between nightlight and population (Thatte et al. 2018), all pixels with value >30 were categorized as urban (towns with a population of more than 50,000 people). Pixels with values between 20 and 30 were categorized as sub-urban (towns with population of 10,000- 50,000 people). The rural expanse that comprises of low house density spread in the mosaic of agriculture and pasture land was obtained using the population density layer (<400 people/ km2 is classified as rural based on the 2011 census of India criteria). The nightlight data and the population density (available at http://www.worldpop.org.uk/ data/get_data/) was obtained for the year 2010 and 2015.

I initially used the index of human settlement derived from nightlight and population density of 2005 and 2010 to project the scenario of 2015 using linear model. This was then compared with the actual data from 2015 to obtain error matrix and overall accuracy (81.82%) and the coefficient of agreement (Kappa index 0.605). I further extrapolate this per pixel trend in settlement expansion for all future scenarios to accommodate demographic projection and the priority in urbanization as per the government's plan of smart cities. The consistent expansion across all the pixels produced by this trend represents the land use pattern under the business-as-usual scenario of future (figure 23). However, increasingly the environmental policies in India are constricting urban expansion inside the protected areas, eco sensitive zones, corridors and important conservation areas (e.g. Hon'ble Supreme court of India's guidelines on curbing tourism in Tiger Reserves). I expect this awareness to limit the future land use conversion inside protected areas and designated wildlife corridors in India. Hence, under the sustainable future scenario, I limit any gain in the night light inside the protected areas and wildlife corridors. To accommodate this increased population, I increase the expansion of the nearest city from a respective protected area so as to follow the contemporary migration patterns of people moving from rural areas to urban areas. I do this by adding the rate of pixel change that were expected inside the protected areas to the nearest city pixels (figure 23).

Food and water security:

Global food demand is projected to double by 2050 (Laurance & Balmford 2013) as a response to increased population demand. India ranks top in World's hunger index, with 14.8% of its population undernourished (FAO et al. 2018). While there is a demand for food production, area under agriculture has reduced by 0.5% since 1980. This naturally pressurizes the existing farmlands for increased productivity, which is chiefly done through irrigation. As a result, irrigated farms have increased 7% in the last two decades, particularly in the drier parts of India like Rajasthan, Maharashtra, and Gujarat. This in turn demands extra water in these water scarce arid and semi-arid landscapes. To achieve these increased demands, various state governments and the central government of India are encouraging water conservation and irrigation in the arid and semi-arid areas of India and construction of dams and canals on various rivers, which mostly originates in the moist forests of India. While irrigation projects in the drier parts are increasing, recent studies highlight water streams depleting from the forests in the Himalaya and the Western Ghats. As a consequence, forests in these regions are getting drier over the last few decades, known as 'browning' of the forests (Krishnaswamy et al. 2014).

For understanding the trends in agriculture over the last two decades, I used Enhanced Vegetation Index (EVI) acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS) from the National Aeronautics and Space Administration (NASA) (Huete et al., 2002) as an index of vegetation cover. I averaged MODIS EVI procured at 16 days' interval at 250 m for last two decades (2001-2018) to index an average vegetation cover. In total, there were 432 temporal replicates for each pixel. This, at first calculates the yearly average variation in the EVI and then the linear regression reduces it for across year comparison to assess the increasing ('greening') or decreasing ('browning') vegetation cover trend for the pixel. This processing was done using the cloud-computing technology in the Google Earth Engine platform, which enables parallel and big data processing required for large study areas. I remove the forest cover derived by the Forest Survey of India (2014) from this product, so as to produce the trend in vegetation apart from forests, which is mostly agriculture or pasture. While, the browning trend in forested areas were used as an index of decreasing water content.

Under the business-as-usual scenario for future, I extrapolate this per pixel trend in agricultural areas to follow the existing pattern for all years (2020, 2030, 2040 and 2050) assuming that the increased population of India will exert pressure to intensify agricultural productivity using biotechnology and other farming practises to maximize the food production (figure 23). This will also index the increased water availability in these areas due to irrigation schemes. For indexing water dynamics under the business-as-usual scenario for forested areas, I used the trend in browning as an index of reduced moisture content; as well as simulate a disappearance of 10% first ordered streams from the forested areas per decade, which has been recorded in the last two decades (Tambe et al. 2012; Tiwari & Joshi 2013) (figure 23). The first ordered streams were derived by hydrological modeling using elevation (SRTM) at 90 m scale, in the SAGA GIS environment (version 2.3.2). For the sustainable future scenario, I consider strategies under the National Mission for Sustainable Agriculture, and micro irrigation fund by the Government of

India that targets maximizing crop production for given ecoregion by promoting native crops and genetically improved varieties (Niti Aayog, 2017). Although it presumes cultivation of drought resistant and genetically enhanced crop varieties, the overall production needs to be in proportion of increasing population. Hence, I retain the trend in greening that is currently observed in the outside-forest India. But due to reduction in the irrigation and other water exhausting projects, I stabilized the browning trend and stream depletion after 2030, as technological revolutions are indicated to be more effective for producing drought resistant crop plants after 2030 (figure 23).

Energy production:

Energy production in India is predominantly driven by coal energy, thereby depends on coal mining. Coal mines in the tropical India are mostly covered by forested areas and mining as resulted in fragmentation and loss of these forests areas. The rate of granting forest clearances has been highest from 2002 to 2011 within the last three decades. 387,952 ha of forest land was diverted during this decade for defence, mining, irrigation, power projects, industries and infrastructure projects (Centre for Science and Environment, 2012). The destruction of 430,000 ha. of standing forest, was recorded due to mining. I derived the existing and potential coal mines from the Greenpeace report (Fernandes 2012) and open government data platform (data.gov.in; Indian Bureau of Mines, Ministry of Mines; Rajya Sabha Session - 248 Unstarred Question No 655; Rajya Sabha Session - 246 Unstarred Question No 1177).

For 'business-as-usual' scenario, I simulate the forest loss due to coal mining in the same quantum that has been the trend for the last two decades (figure 23). This trend is supported by few of the recent amendments by the Government of India in the Mines and Minerals (Development and Regulation) Act in 2015, which ordered to expedite environmental clearances and issuance of licenses. For 'sustainable future' scenario, I use the trend in sustainable energy alternatives encouraged in India. It is projected that growth in the region's coal use will halt after 2025 and peak around 2030. To some extent, India is leapfrogging coal to get directly to renewable power. From 2030, it is projected to install 100-150GW of new solar capacity every year, and photovoltaic's share in total power generation will reach almost 60% before levelling off at the highest share in any world region (figure 23). State-level policies such as the Gujarat Solar Policy further support this projection in the energy sector.

Global climatic change:

To address the effect of ongoing global climatic changes, I utilized the bioclimatic layers from Worldclim ver. 1 that are known to significantly influence the invasive plants distribution as established in Chapter 4, 5 and 6. I used temperature of the coldest month, temperature of the warmest quarter, annual precipitation, and precipitation of the wettest and driest quarter. The climatic variables were kept constant for 2010-2020, 2030-2040, and 2050. These future variables were obtained for 2030 and 2050 from the fifth Assessment Report of the International Panel of Climate Change (AR5, IPCC) (Stocker et al. 2013) for India. I used climatic scenarios for the two Representative Concentration Pathways (RCPs), which represent two greenhouse gas concentration scenarios based on the projection of human demographics and socio-economic conditions at the end of this century (Moss et al. 2010). RCPs vary from the most 'sustainable-future' scenario of reduced greenhouse gas emissions after 2020 to the end of century, to the 'business-as-usual' scenario that assumes emission to increase with the present trend till 2100 (Van Vuuren et al. 2011) (figure 23). The scenarios were developed under Community Climate System Model version 4 (CCSM4) released by the National Centre for Atmospheric Research (NCAR), which includes improvements in the treatment of clouds, aerosols, and land and sea surface temperatures.

Invasive species management:

The rates of invasion by the study species were estimated in chapter 6, which suggests that these plants spread significantly around previously occupied sites. Hence, the current trend of removing invasive species from priority sites can reduce their spread. Presently, invasive species management is targeted in areas with high conservation value for sustaining charismatic species. Through my personal observation across 14 Tiger Reserves, 6 National Parks, 11 Wildlife Sanctuaries, more than 30 Reserve and Territorial Forest Divisions in the tropical India, I observed that most of the invasive species management is done in the core area of Tiger Reserve, followed by National Parks, Wildlife Sanctuaries, Buffer zone of Tiger Reserve, and least in the Reserve and Territorial forest divisions. Summary on the spatial and temporal management actions taken at 95 sites across the tropical India is provided in table 25.

In order to understand the efficacy of invasive species management in arresting the spread of invasive species, I simulated the spatio-temporal trend in the observed management pattern across different forest types in tropical India. Under the 'business-as-usual' scenario for future, I retained the spatio-temporal frequency of invasive species management in different forest types across the tropical India. For doing so, I proportionately simulated the management site based on the forest and protected area type in the tropical India. The frequency of management was also based on the forest type considered. However, none of the observed management case was for an area more than 1 km^2, which is the present study scale. Hence, I took a conservative estimate of considering the entire pixel as managed in the simulated sites (figure 23). Under the 'sustainable future' scenario, I doubled the rate of management sites in the present protected and forest types, as well as added the existing trend observed in different forest types of Tiger Reserve buffer to Reserve and Territorial forest divisions and wildlife corridors (figure 23). In both the scenarios, after removing the simulated managed sites, I estimated Euclidean distance of each pixel from the nearest invaded site using ArcGIS (Ver. 10.6.1) and used it as an explanatory covariate.

Table 25 Area managed for different invasive plants across the forest and protected area type in tropical India

Protected area type	Forest type	Average management sites per year	Average area managed (in ha.)
Tiger Reserve core	Grasslands	18	8
Tiger Reserve core	Scrub	14	6
Tiger Reserve core	Open forest	7	2
Tiger Reserve core	Moderately dense forest	4	1
Tiger Reserve core	Dense forest	3	1
Tiger Reserve buffer	Grasslands	4	3
Tiger Reserve buffer	Scrub	8	5
Tiger Reserve buffer	Open forest	5	2
Tiger Reserve buffer	Moderately dense forest	3	1
Tiger Reserve buffer	Dense forest	2	1
National Park	Grasslands	13	9
National Park	Scrub	9	5
National Park	Open forest	5	3
National Park	Moderately dense forest	7	2
National Park	Dense forest	3	1
Wildlife Sanctuary	Grasslands	7	3
Wildlife Sanctuary	Scrub	6	2
Wildlife Sanctuary	Open forest	4	1
Wildlife Sanctuary	Moderately dense forest	1	1
Wildlife Sanctuary	Dense forest	2	1
Territorial forest	Grasslands	0.5	0.25
Territorial forest	Scrub	0	0
Territorial forest	Open forest	0.25	0.5
Territorial forest	Moderately dense forest	0	0
Territorial forest	Dense forest	0	0

Species Distribution Modelling

To get an estimate of invasive plants distribution across the region, I used Maximum Entropy (MaxEnt) (Phillips et al. 2004), one of the most widely used algorithms for distribution modeling. MaxEnt calibrates environmental variables from species presence locations and compares them with a set of random sample locations from the study area (Presence-background model). It uses this calibrated relationship of species presence with environment variables to seek similar locations that would likely support the target species. The most unconstrained model developed is considered as the MaxEnt model. I divided the presence data of each species into training (80%) and testing (20%) sets, using k-fold partitioning design, with k=5. I used each k-partitioned set, for every species, as an input data for MaxEnt. Subsequently, in order to avoid the autocorrelation within the input data, it was filtered so as to select only one presence point from a pixel (1 km^2). Statistically, MaxEnt is a presence-background model that compares the presence locations with available environmental space. The range of background environment substantially influence the response curve and subsequent modelled distribution, which necessitates appropriate ecological criteria and sampling strategy to define the background (Elith et al. 2010, Webber et al. 2011). Since I only consider forested landscapes for this study, background points were obtained only from the forested areas of India. I modelled the kernel density of the presence locations and used this surface to select background points. Within the forests of this surface, I randomly selected 10,000 points to estimate the background environment. Similar to the filtering of input data, only one background point was selected from a pixel.

I used linear, quadratic, hinge and product features to generate the MaxEnt model with 100 replicates for each species. This model was projected to the two alternate future scenarios under that represent the changes brought to the forest under the 'business-as-usual' scenario and the 'sustainable-future' scenario.

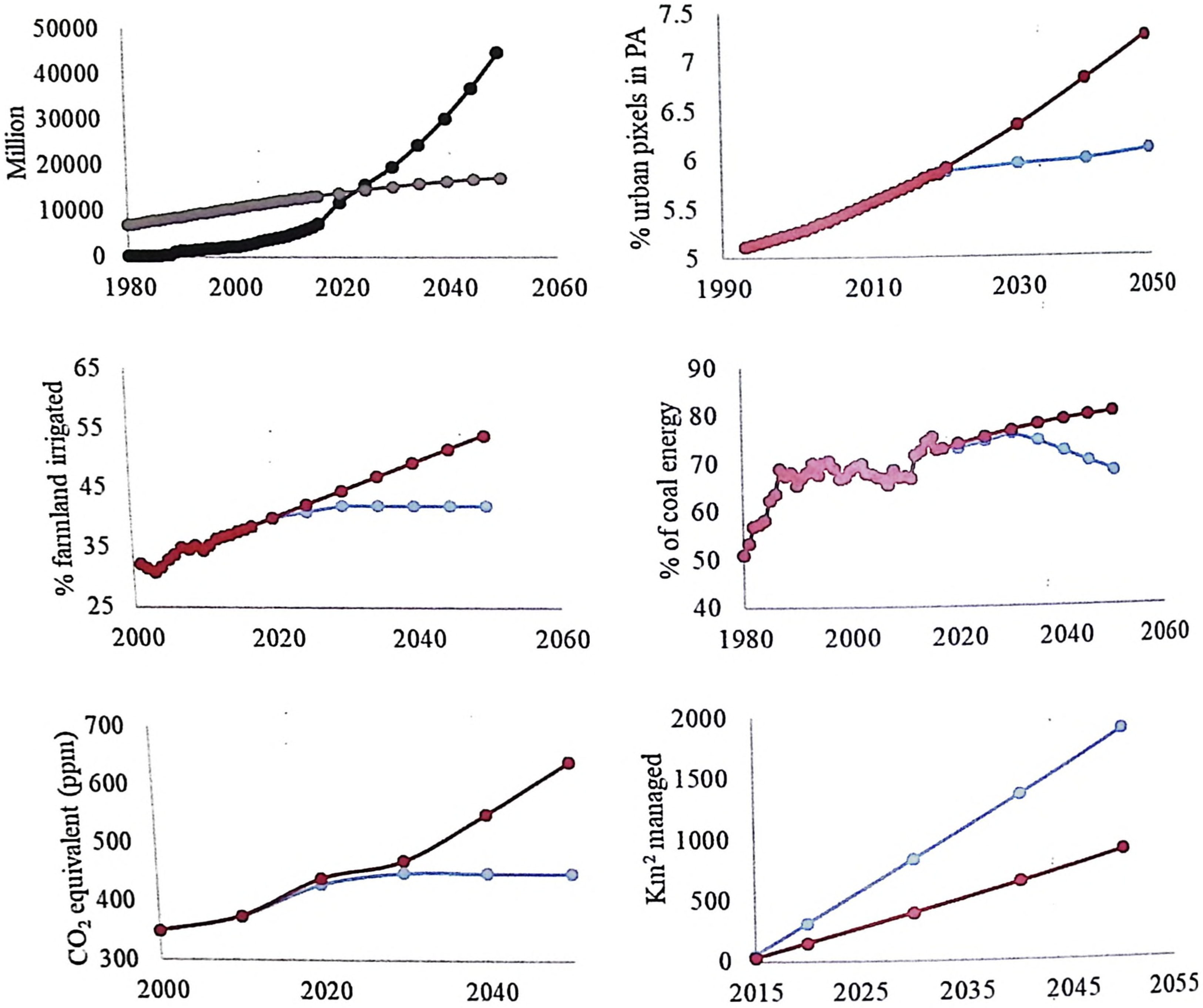


Figure 25 Future projection of landscape drivers for invasive plants under the 'business-as-usual' model (red) and 'sustainable future' model (blue)

However, the future scenarios might result in a combination that is presently unavailable. Extrapolating the distribution to such an environmental combination has statistical limitations, hence I avoided that by removing all such novel areas. I model the novel areas by using four different methods: NicheA (Escobar et al. 2016), Mobility-Oriented Parity (MOP) (Owens et al. 2013), Multivariate Environmental Similarity Space (MESS) (Elith et al. 2010) and ExDent tool (Mesgaran et al. 2014). These methods are already elaborated in chapter 4.

Any bias correction protocol was not required, as the data was systematically collected across the study area. Area Under the receiving operating characteristic Curve (AUC) of MaxEnt model was considered as an additional criterion to assess the ability of MaxEnt model to predict invasive plants presence. MaxEnt produces niche probability for every pixel that varies from 0 to 1. In the present study, all pixels of the output raster that were greater than a threshold that had highest True Skill Statistics (TSS), were considered as presence. To assess the TSS, I used the 20% test data retained initially and the true absence data recorded as that location, where the species has been absent consistently across the sampling period (2006-2018). I average the results of all the k-partitioned model runs, for each species. The present distribution estimate of each species was compared with its projected distribution under the alternate future models.

I initially built the model of the year 2006 using the contemporary covariates and project the distribution of invasive plants in 2018 using the covariates of year 2018. I use the presence location of invasive plants from the sampling cycle of 2018 to validate the modelled projection. I assess the difference in the modelled and observed distribution of invasive plants in 2018 to understand the error limit and error direction in the future projections. After obtaining the projected distribution for each year, I modelled the total change in area by adding the new invaded areas and previous invaded areas. This was based on the assumption tested in the chapter 4 and 6, where I showed that the species tend to adapt with the local environment due to within plasticity. Hence, I do not expect it to contract its niche due to fluctuations in the external environment, on the contrary I show in chapter 4 that the species utilizes novel niche across their biogeographic range. The only deviation to this trend of expansion in species spread is for *Parthenium hysterophorus*, whose distribution was observed to be reduced in the last 12 years; presumably due to biocontrol agents. I did similar projection by using only climatic changes, while keeping the landscape level covariates constant. This was for understanding the pervasive threat of global climatic changes against the regional drivers aspired by the national politics and social choices.

Results:

The MaxEnt models had an overall accuracy of 0.72 (±0.6), as validated using TSS. Distance from the nearest invaded sites had maximum average contribution to overall species (0.27±0.08), followed by annual rainfall (0.19±0.1), night time lights (0.13±0.04), temperature of the coldest month (0.11±0.06), the temperature of the warmest quarter (0.1±0.05), precipitation of the driest quarter (0.09±0.04), water depletion (0.07±0.06), mining (0.04±0.04), and agricultural greening (0.03±0.02). The areas in future India, which have novel environmental combinations that are absent in present India were removed from the future projections.

After modelling the distribution of invasive plants as a function of these covariates from the data of 2006 and projecting it to 2018, using contemporary changes in covariates, I assessed the difference in projected and observed distribution of the invasive plants. The difference is shown in figure 24. Apart from *Ageratum conyzoides, Hyptis suaveolens* and *Parthenium hysterophorus*, all other species projection was less than the observed distribution in 2018. This suggests that the future projections are conservative estimates of what might happen.

The distribution trend of invasive plants in India under the projected future scenarios are provided in figure 25. The distribution of all invasive plants under the business-as-usual scenario was consistently higher as compared to sustainable future scenario. Although, the distribution under any scenario was projected to be more than double of the present distribution. The highest area under the business-as-usual and sustainable future scenario was invaded by *Lantana camara,* followed by *Prosopis juliflora* and *Senna tora.* When only global climatic changes were considered by keeping all landscape drivers constant, the expansion of invaded areas reduced by 40 (±8) % as compared to the scenarios in which both climatic and landscape drivers were changed (figure 26). The highest area was projected to be invaded by the same three species viz. *Lantana camara, Prosopis juliflora* and *Senna tora.* However, the difference in the projected area under the business-as-usual scenario and sustainable future scenario was higher when only climatic changes were considered (figure 26), as compared to when landscape changes were considered as well (figure 25). With all drivers considered, the average distance between the projections under business-as-usual and sustainable future scenario was 363,158 km^2 in 2030; 538,617 km^2 in 2040 and 597,867 km^2 in 2050 (figure 25). With only climatic changes considered, the average difference amongst the species was 353,280 km^2 in 2030; 584,392 km^2 in 2040 and 827,932 km^2 in 2050 (figure 26).

When the projected distribution under the overall changing landscape was compared with the forest types and biogeographic zones in India, I observed that the dry forests of central India was the highest invaded forest type by *Lantana camara, Senna tora, Hyptis suaveolens* and *Xanthium strumarium* (figure 27). The dry savanna of the tropical India was second highest invaded category, particularly by *Prosopis juliflora, Senna tora, Parthenium hysterophorus* and *Xanthium strumarium* (figure 27). The moist forests of the Western Ghats were predominantly invaded by *Chromolaena odorata* and *Mikania micrantha*; while in the Shivalik and terrai were invaded by *Ageratina adenophora, Lantana camara* and *Mikania micrantha*. Northeastern hills had the least projected invasions (figure 27). When only climatic changes were considered, all forest types in the Western Ghats and moist forests in Central India had the highest expansion in invaded areas, particularly by *Lantana camara, Senna tora, Chromolaena odorata* and *Mikania micrantha*. Least invasion was again observed in the Northeastern hills. The largest difference in invasion was in Central Indian dry forests, where the area invaded was reduced when only climatic changes were considered.

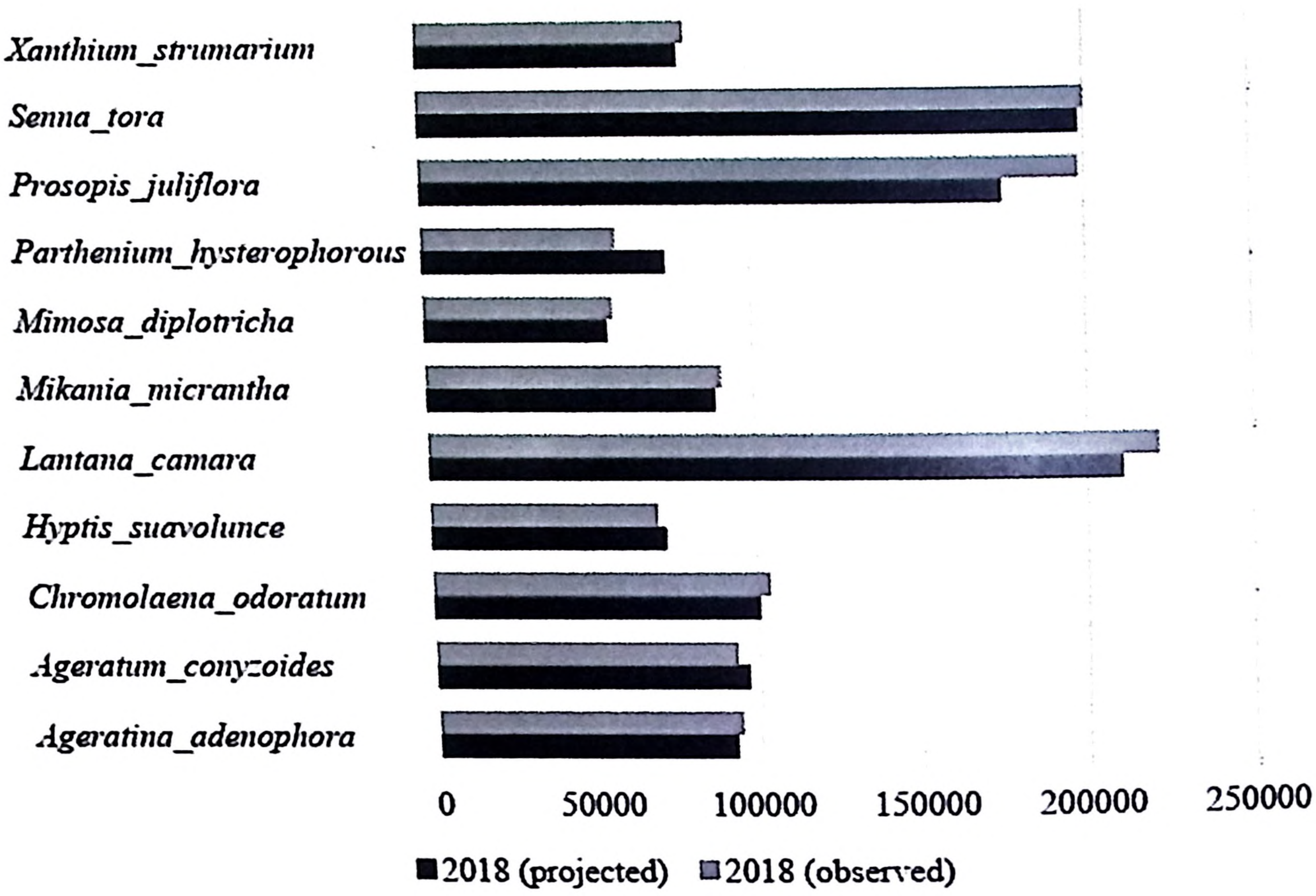


Figure 26 the difference in projected and observed area under invasion of different plants in the year 2018

Discussion:

The results suggest that invasive plants could invade more than 90% of the existing forest cover, apart from the savanna and grasslands that are not yet completely mapped. The expansion of invasive plants was highest when business-as-usual scenario was considered with all landscape drivers changing. The expansion was minimal under the sustainable future scenario with all landscape drivers constant with only climatic changes with reduced emission. The sustainable future scenario under with all landscape drivers changing had higher invasion threat for many species, when compared with the business-as-usual scenario with only climatic changes. This clearly indicates that the models adopted under the category of sustainable future aren't able to safeguard the natural floral composition of India from invasive plants.

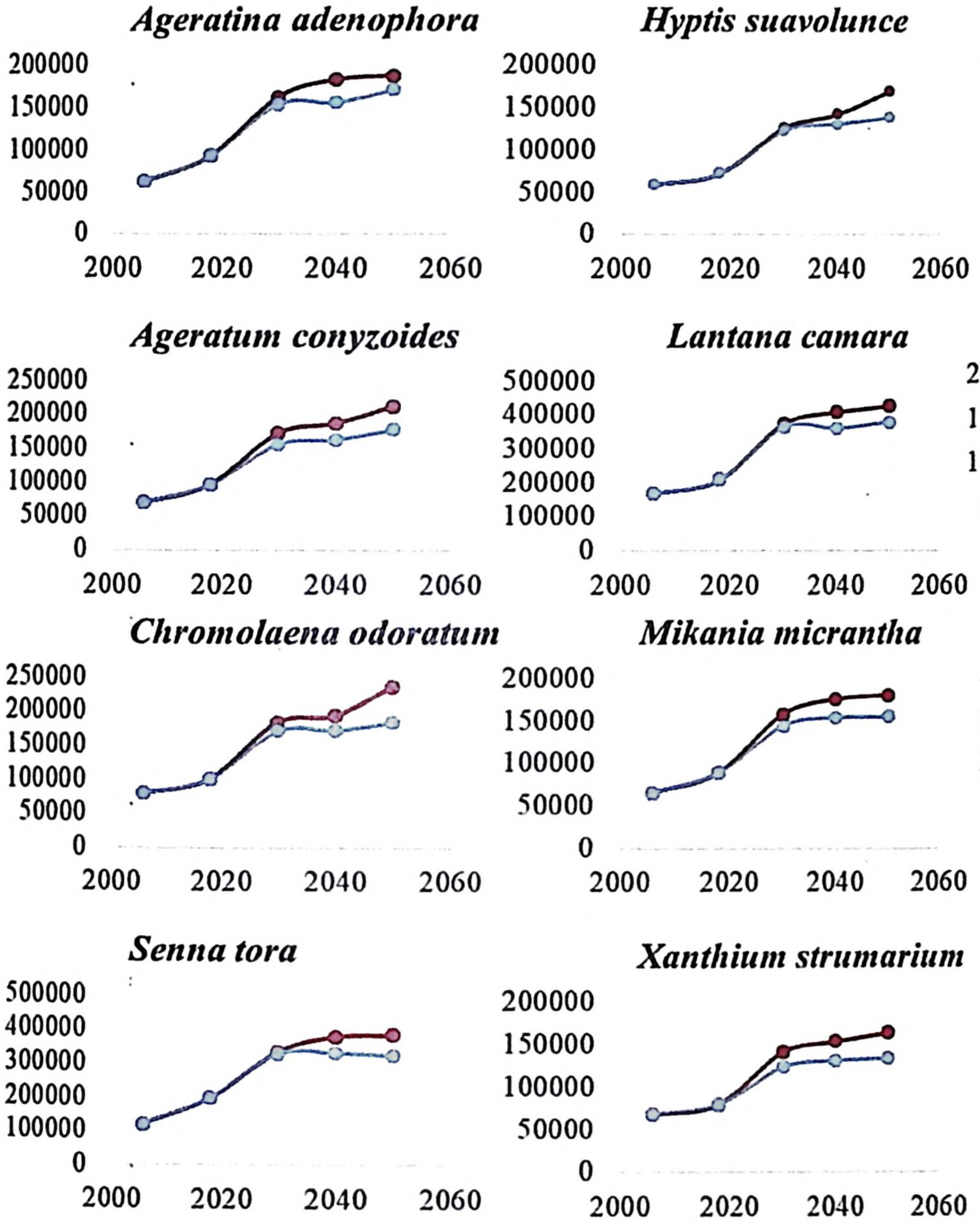


Figure 27 Projected area invaded by the invasive plants under the 'business-as-usual' model (red) and 'sustainable future' model (blue). Here all landscape drivers were considered that includes urbanization index, agricultural expansion, water security, mining, climatic changes and invasive plant management

The present study results demonstrate that by curbing mining in the central Indian landscape, at least 42000 km2 forests could be saved, which could be else invaded by different invasive plants, mostly *Lantana camara, Senna tora, and Hyptis suaveolens*. Similarly, a consistent high invasion in savannas was due to the agricultural productivity enhanced by irrigation plans under both the alternate future scenarios. This in particular facilitated invasion of *Prosopis juliflora, Senna tora, Parthenium hysterophorus* and *Xanthium strumarium*. Fire and loss of water

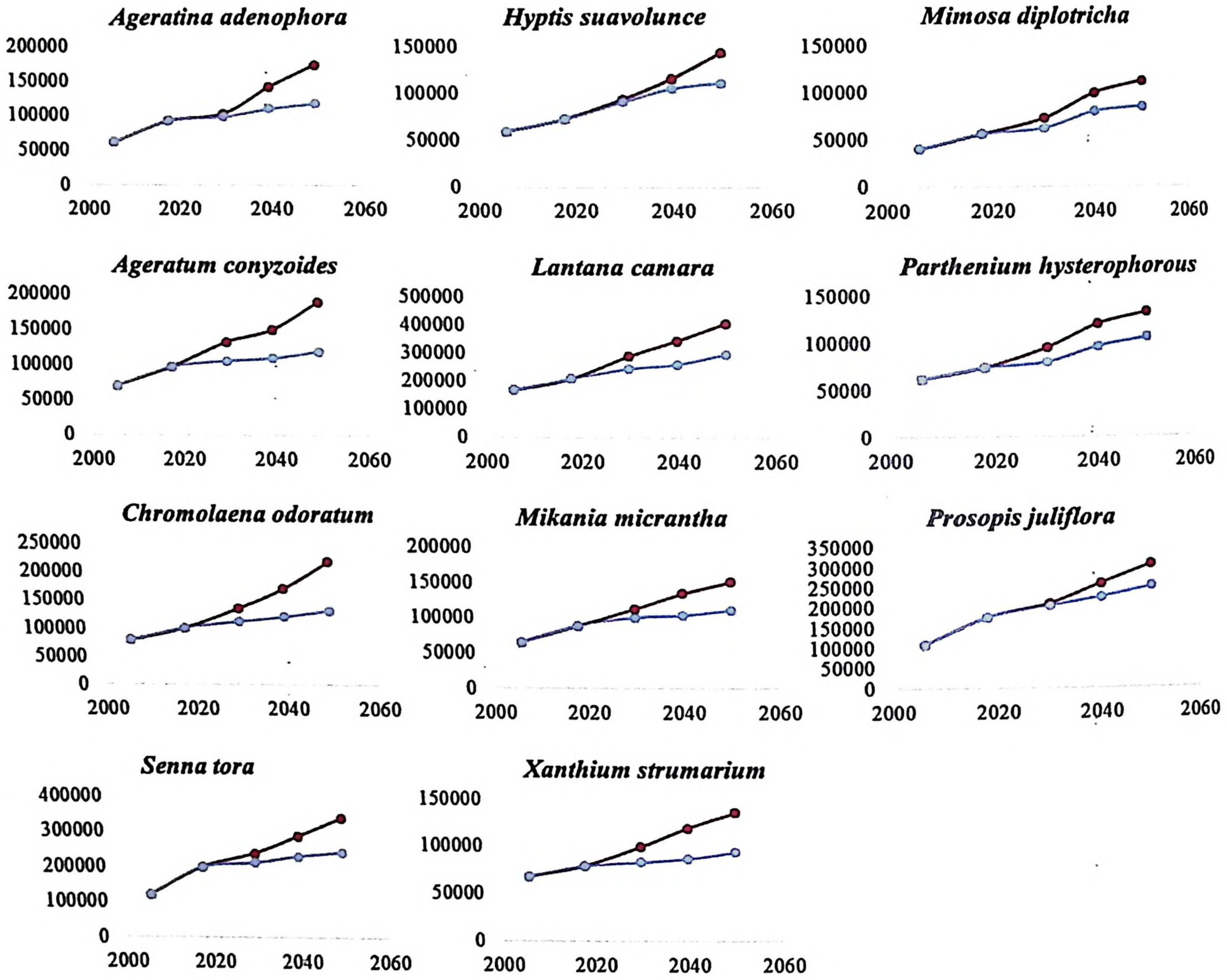
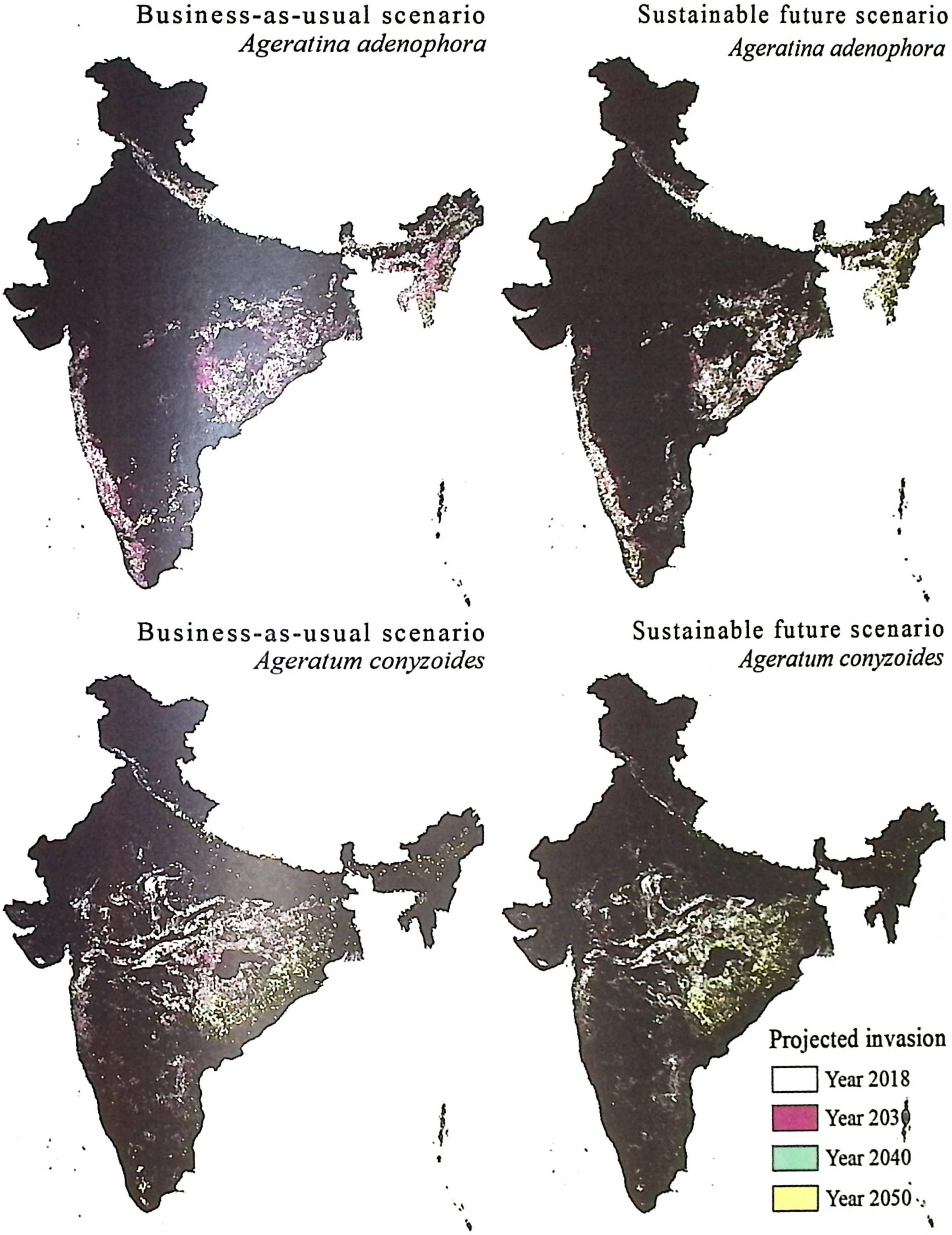
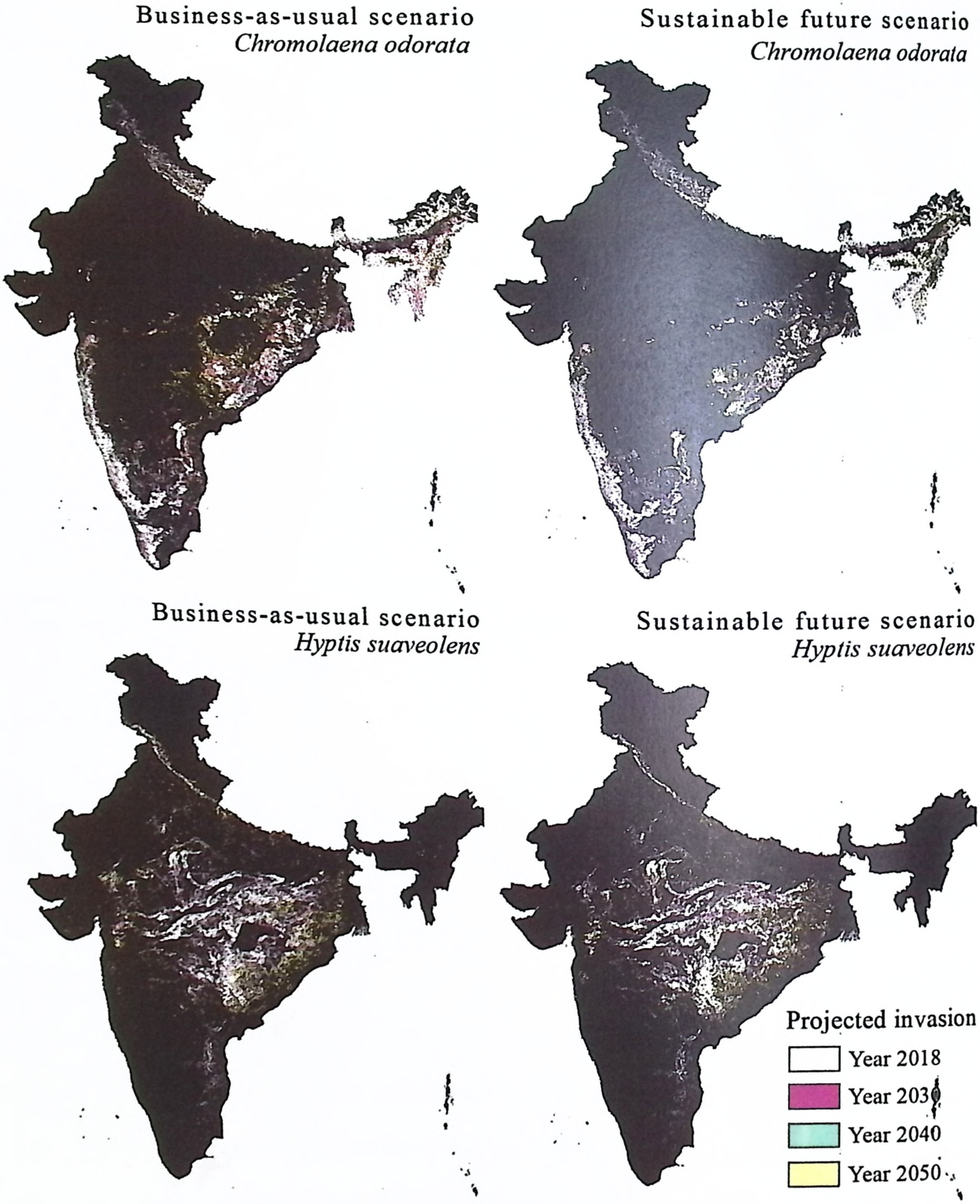


Figure 28 Projected area invaded by the invasive plants under the 'business-as-usual' model (red) and 'sustainable future' model (blue). Here only global climatic changes were considered, keeping all other drivers constant to understand the effect of only climatic changes on the forests of India

facilitated the invasion of *Ageratina adenophora, Chromolaena odorata and Mikania micrantha* in the Shivalik-terai landscape and Moist forests of Western Ghats. Northeastern hills had consistently less invasion under any scenario, which could also be due to less presence data on the status of invasive plants in this area. But it also indicated that areas that have less urban footprint (night time lights) or agricultural and mining pressure can retain its composition from being invaded. Our results also suggest that by reducing the urban expansion under the current protected areas, we could safeguard the area from invasive plants. Thus, protected areas can be a key to safeguard the natural areas even in the recent future.


Business-as-usual scenario
Ageratina adenophora
Sustainable future scenario
Ageratina adenophora
Business-as-usual scenario
Ageratum conyzoides
Sustainable future scenario
Ageratum conyzoides
Projected invasion
Year 2018
Year 2030
Year 2040
Year 2050

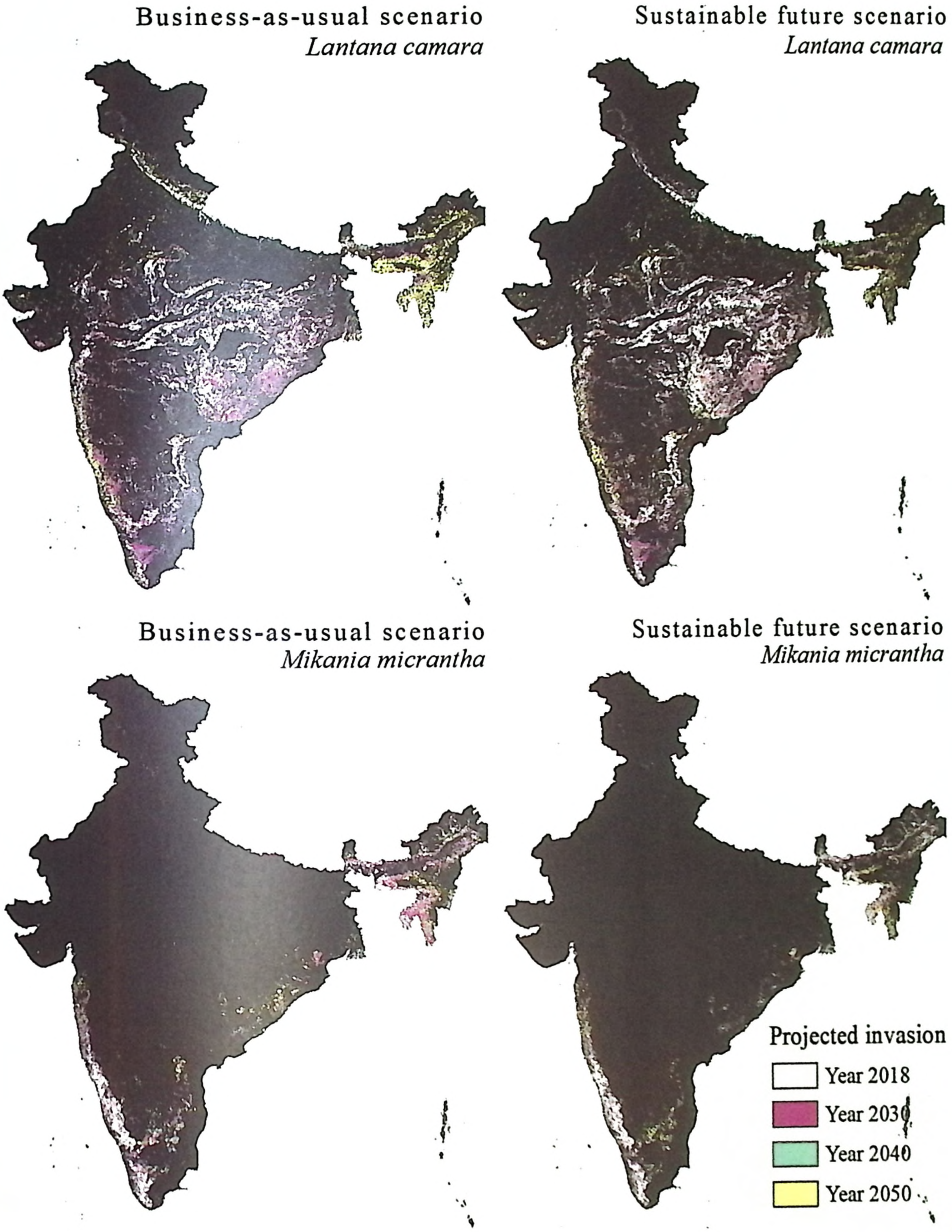


Business-as-usual scenario
Chromolaena odorata

Sustainable future scenario
Chromolaena odorata

Business-as-usual scenario
Hyptis suaveolens

Sustainable future scenario
Hyptis suaveolens



Business-as-usual scenario *Lantana camara*

Sustainable future scenario *Lantana camara*

Business-as-usual scenario *Mikania micrantha*

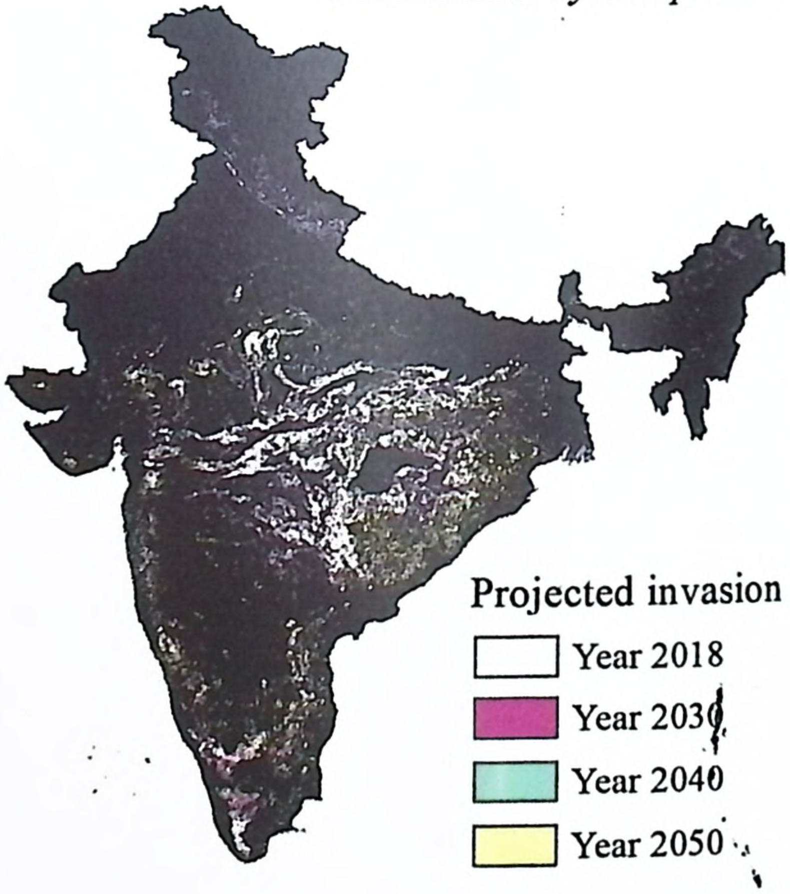
Sustainable future scenario *Mikania micrantha*

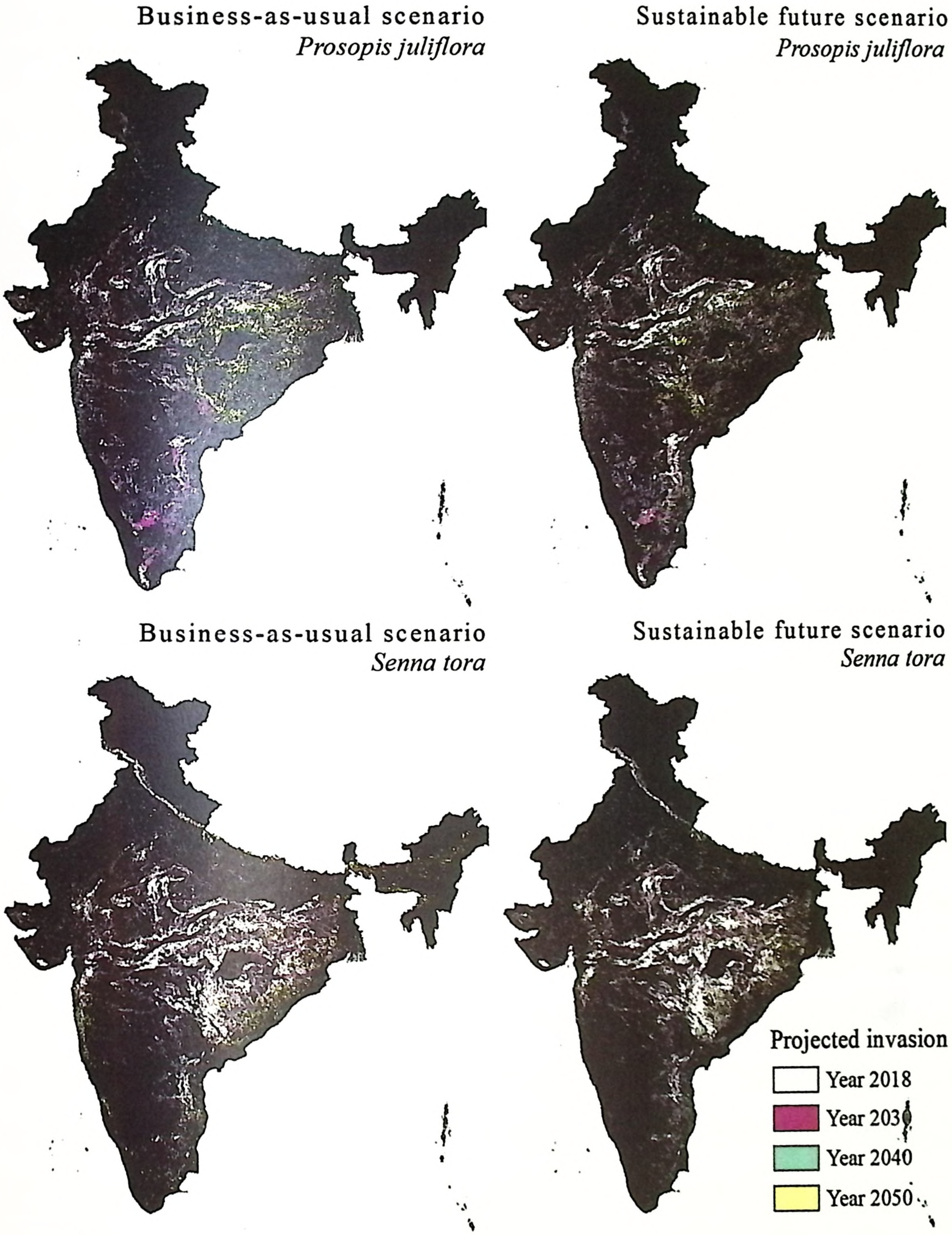
Business-as-usual scenario
Mimosa diplotricha

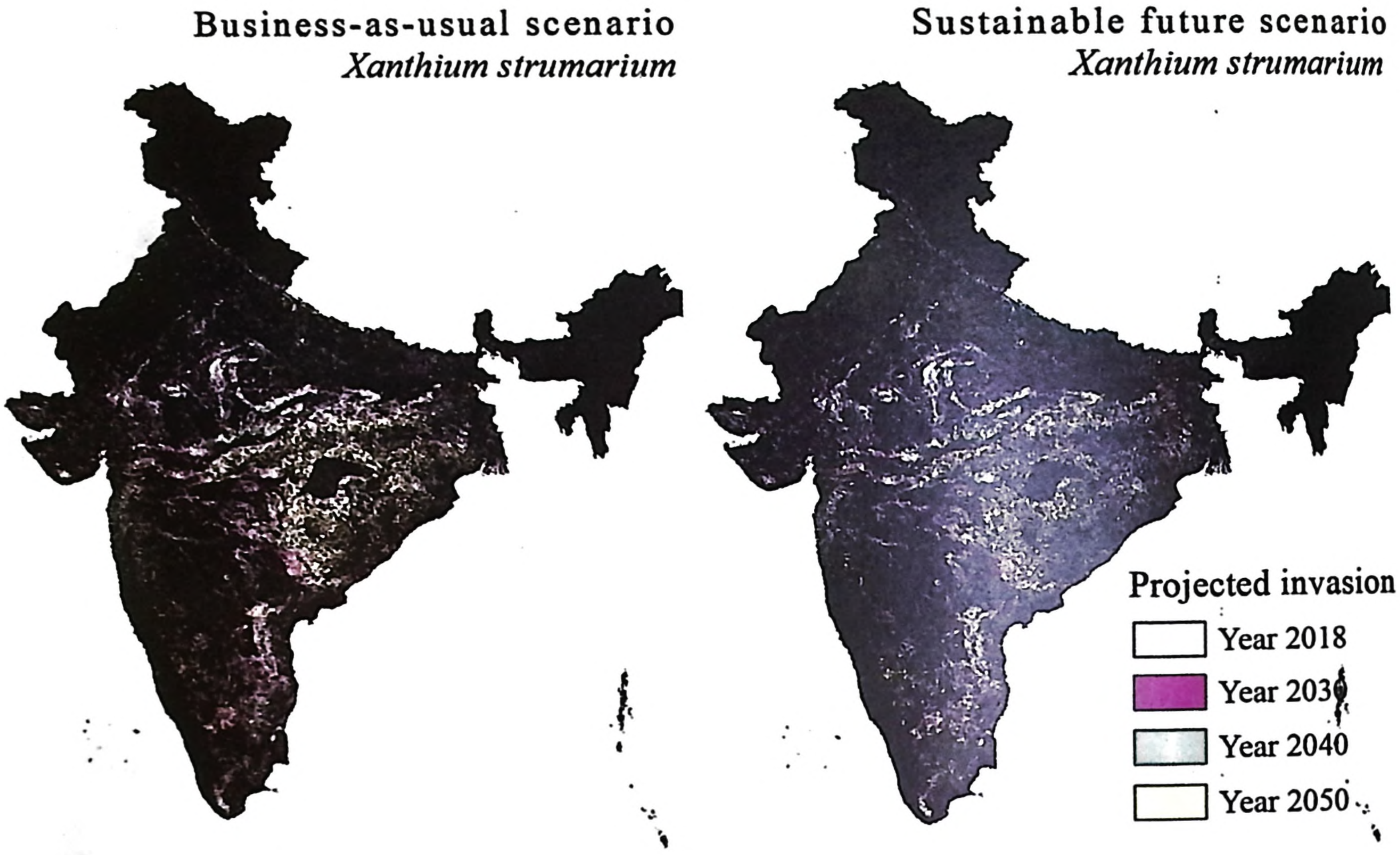
Sustainable future scenario
Mimosa diplotricha

Business-as-usual scenario
Parthenium hysterophorus

Sustainable future scenario
Parthenium hysterophorus




Business-as-usual scenario
Prosopis juliflora
Sustainable future scenario
Prosopis juliflora
Business-as-usual scenario
Senna tora
Sustainable future scenario
Senna tora
Projected invasion
□ Year 2018
🟥 Year 2030
🟩 Year 2040
🟨 Year 2050


Business-as-usual scenario
Xanthium strumarium

Sustainable future scenario
Xanthium strumarium

Figure 29 Future projections of area under invasive plants in India under the 'business-as-usual' and 'sustainable future' scenario, with all important landscape drivers considered

Even after doubling the management sites for invasive plants, there wasn't any significant change in the invasion trend for any species. Currently, around 98,000 INR is required for managing a species at 1 km^2(Love et al. 2009); and around 24 crore INR is projected to be spent (ideally) for managing invasive plants (Mungi et al. 2020). Even doubling the area and the cost could not make any significant difference in reducing the area under invasion. This result should be considered in the light of two aspects, invasive plants are required to be managed at priority sites, and invasive plants tend to expand around sites that are already occupied. As our results suggest, due to lower urbanization in the protected areas and wildlife corridors, the invasion expansion might be lower. Moreover, currently protected areas have disproportionately higher densities of many flagship species that requires healthy habitat quality. Hence, a planned strategy to eradicate invasive plants by considering the protected areas and corridors, in a way where areas surrounding invaded sites are systematically cleared to reduce further expansion. The strong limitation to this approach remains in the fact the present protected area network is mainly in the forested areas, while savanna and dry forests might remain predominantly outside the traditional protected areas or natural areas. Hence, there is a requirement to recognize this ecological category as one of the most vulnerable type to the invasion pressure, and to safeguard it by further investigating on the priority sites, control efficacy and frequency of management.

While in India, where forest fragmentation is miniscule as compared to many other tropical countries, the threat of invasive plants was modelled as pervasive. Other countries where forest clearing and fragmentation is rampant, invasive species expansion remains a major unseen threat, particularly in the wake of global climatic changes. Unlike India, where a large-scale repeated sampling is missing, this threat can be undetected. With the known trend of expansion in invasive plant, many tropical and subtropical countries could already be affected by invasive species. There is a requirement to monitor the status of natural areas at large-scale and control the expansion of invasive plants, particularly around the invaded areas. I further show that many local stressors (e.g. mining) interact with global climatic changes and facilitate the expansion of invasive species. hence, rather than preventing either or stressors, there is a requirement of preventing the rapid changes happening at all the spheres. The future projection also revealed that regional actions for mitigating the increased invasion may not be adequate as the majority of the range expansion occurs as a response to change in global climatic scenarios. As recent global climatic changes are manifestation of human induced local disturbances, adopting a proactive control measures for such disturbances in place of reactive mitigation measures is globally needed to sustain the ecological integrity and allied services. Thus, more policy actions are needed at the global scale for reduction in greenhouse gases emission to avoid similar range expansion and collapse of native ecological communities worldwide.

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Appendix 1 (chapter 2): Criteria and scores for reviewing the information available on three modules viz. Potential, Impact and Management of High Concern Invasive Species in India

Module and Criteria	**Criteria**	**Score**
MODULE A: POTENTIAL OF INVASION		
a) Dispersal	No	0
Species have a potential for long distance dispersal	Yes	1
b) Invasive elsewhere	Yes	1
Species has invaded different biogeographic regions	No	0
c) Recolonization Potential	No recolonization	0
What is the degree of species recolonizing the restored region?	Occasionally recolonization	1
	Restored area need frequent management due to high recolonization pressure	2
d) Dispersal Agents	Either Abiotic or Biotic	1
How is species dispersal to new area aided?	Both biotic and abiotic	2
e) Density	Individuals	1
How does the species grow in an invaded region?	Small clumps	2
	Vast homogenous stands	3
	Mixed stands with other invasive	4
f) Spatial Distribution	<50% grids	1
Out of the potential area in the country, how many grid cells (scale 1° x 1°) were occupied?	>50% grids	2
	>80% grids	3
	No information available	4
MODULE B: IMPACTS		
g) Impacts on biodiversity	None	0

What is the degree of impact on biodiversity of invaded region?	Impact on taxa/ecosystem (direct and indirect)	1
	Depressed population to individual extinction	2
	Ecosystem restructuring	3
	Information not available	NA
h) Impacts on physical features *What is the degree of impact on the physical features (habitat structure) of invaded region?*	None	0
	Minor changes	1
	Significant changes	2
	Information not available	NA
i) Impacts on ecosystem services *What is the degree of impact on ecosystem services of invaded area?*	None	0
	Disruption of one ecosystem service	1
	Disruption of more than one ecosystem service	2
	Information not available	NA
j) Positive economic impact *In case people are procuring benefits due to the invasive species, what is the scale of economic benefit?*	No positive economic impact	0
	Occasional use by communities	1
	Frequent use for small business	2
	Frequent use for commercial purpose	3
	Utilized by more than one sector	4
	Information not available	NA

MODULE C: MANAGEMENT

k) Chemical Control *Whether species can be controlled by the use of chemical agents?*	Not available	3
	Impractical due potential harmful effects	2
	Practically successful	1
	Effective and economically feasible	0
l) Mechanical Control *Whether species can be controlled mechanically?*	Not available	3
	Impractical due to logistic constraints	2
	Practically successful	1
	Effective and economically feasible	0
m) Biological Control	Complete control	0

Whether species can be controlled using biological control agents?	Substantial control	1
	Negligible control	2
	No biological control agents released	3
n) Restoration *In what magnitude are the efforts for restoration needed?*	Active restoration needed	3
	Passive restoration needed	2
	No restoration required	1
o) Legislation Are policies and guidelines in place to manage invasive species?	Policies are available with clear directions for concerned agencies	0
	No policies; guidelines are available with identification of responsible agencies	1
	Management of Invasive species is a part of larger policy	2
	No policies or guidelines available	3
p) Identification of stakeholders Are stakeholders identified for effective management?	System in place	0
	No directives to the identified stakeholders	1
	Stakeholders not identified.	2
q) Potential conflicts Can management of invasive species cause conflict within stakeholders?	Conflict envisioned	1
	No conflict envisioned	0

11

Appendix 2: Pearson's corelation amongst environmental covariates. Highlighted values had higher correlation (-0.7 > r > 0.7).

Layer	aridity	b1	b12	b13	b14	b16	b17	b5	b6	dem	df	dg	dnl	droad	dwat	fh	hp	lvsn	ndvi april	ndvi diff	ndvi oct	nitlit	ept	rugg
aridity	1.00	-0.38	0.95	0.82	0.19	0.86	0.25	-0.62	-0.07	0.08	-0.09	0.21	0.13	0.09	0.15	0.14	-0.12	-0.26	0.60	-0.43	0.37	0.00	-0.58	0.18
b1	-0.38	1.00	-0.27	-0.11	-0.38	-0.14	-0.41	0.78	0.73	-0.85	0.14	-0.25	-0.39	-0.36	-0.44	-0.17	0.39	0.25	-0.47	0.28	-0.34	0.02	0.76	-0.79
b12	0.95	-0.27	1.00	0.92	0.10	0.95	0.16	-0.53	0.03	-0.01	-0.10	0.20	0.10	0.04	0.10	0.13	-0.07	-0.24	0.57	-0.40	0.37	0.00	-0.47	0.09
b13	0.82	-0.11	0.92	1.00	-0.15	0.99	-0.11	-0.30	0.16	-0.04	-0.08	0.07	0.06	-0.05	-0.03	0.07	0.00	-0.16	0.37	-0.24	0.25	-0.01	-0.20	0.00
b14	0.19	-0.38	0.10	-0.15	1.00	-0.10	0.92	-0.45	-0.19	0.24	-0.08	0.23	0.12	0.15	0.17	0.13	-0.15	-0.20	0.43	-0.33	0.25	0.01	-0.45	0.33
b16	0.86	-0.14	0.95	0.99	-0.10	1.00	-0.05	-0.33	0.09	-0.05	-0.10	0.11	0.08	-0.01	0.00	0.08	-0.03	-0.19	0.40	-0.25	0.28	-0.01	-0.28	0.01
b17	0.25	-0.41	0.16	-0.11	0.92	-0.05	1.00	-0.48	-0.27	0.18	-0.08	0.29	0.09	0.13	0.21	0.15	-0.14	-0.21	0.50	-0.38	0.29	0.01	-0.53	0.30
b5	-0.62	0.78	-0.53	-0.30	-0.45	-0.33	-0.48	1.00	0.26	-0.55	0.08	-0.30	-0.26	-0.22	-0.42	-0.19	0.23	0.26	-0.77	0.61	-0.43	0.00	0.84	-0.62
b6	-0.07	0.73	0.03	0.16	-0.19	0.09	-0.27	0.26	1.00	-0.53	0.12	-0.13	-0.30	-0.34	-0.35	-0.08	0.40	0.16	-0.03	-0.12	-0.16	0.02	0.45	-0.46
dem	0.08	-0.85	-0.01	-0.04	0.24	-0.05	0.18	-0.55	-0.53	1.00	-0.11	0.11	0.34	0.30	0.33	0.08	-0.29	-0.14	0.19	-0.10	0.16	-0.03	-0.47	0.82
df	-0.09	0.14	-0.10	-0.08	-0.08	-0.10	-0.08	0.08	0.12	-0.11	1.00	-0.20	-0.16	-0.12	-0.16	0.12	0.30	0.20	-0.23	-0.17	-0.47	0.04	0.11	-0.20
dg	0.21	-0.25	0.20	0.07	0.23	0.11	0.29	-0.30	-0.13	0.11	-0.20	1.00	0.29	0.22	0.30	0.14	-0.36	-0.18	0.45	-0.15	0.45	-0.04	-0.32	0.23
dnl	0.13	-0.39	0.10	0.06	0.12	0.08	0.09	-0.26	-0.30	0.34	-0.16	0.29	1.00	0.60	0.25	0.12	-0.47	-0.17	0.21	-0.02	0.25	-0.08	-0.28	0.40
droad	0.09	-0.36	0.04	-0.05	0.15	-0.01	0.13	-0.22	-0.34	0.30	-0.12	0.22	0.60	1.00	0.21	0.10	-0.36	-0.12	0.12	0.02	0.18	-0.04	-0.26	0.35
dwat	0.15	-0.44	0.10	-0.03	0.17	0.00	0.21	-0.42	-0.35	0.33	-0.16	0.30	0.25	0.21	1.00	0.01	-0.31	-0.17	0.35	-0.14	0.32	-0.03	-0.43	0.39
fh	0.14	-0.17	0.13	0.07	0.13	0.08	0.15	-0.19	-0.08	0.08	0.12	0.14	0.12	0.10	0.01	1.00	-0.14	-0.06	0.14	-0.26	-0.06	-0.01	-0.16	0.12
hp	-0.12	0.39	-0.07	0.00	-0.15	-0.03	-0.14	0.23	0.40	-0.29	0.30	-0.36	-0.47	-0.36	-0.31	-0.14	1.00	0.20	-0.21	-0.05	-0.33	0.12	0.29	-0.41
lvsn	-0.26	0.25	-0.24	-0.16	-0.20	-0.19	-0.21	0.26	0.16	-0.14	0.20	-0.18	-0.17	-0.12	-0.17	0.06	0.20	1.00	-0.26	0.09	-0.25	0.01	0.25	-0.17
ndvi april	0.60	-0.47	0.57	0.37	0.43	0.40	0.50	-0.77	-0.03	0.19	-0.23	0.45	0.21	0.12	0.35	0.14	-0.21	-0.26	1.00	-0.65	0.68	-0.01	-0.68	0.37
ndvi diff	-0.43	0.28	-0.40	-0.24	-0.33	-0.25	-0.38	0.61	-0.12	-0.10	-0.17	-0.15	-0.02	0.02	-0.14	-0.26	-0.05	0.09	-0.65	1.00	0.11	-0.03	0.44	-0.17
ndvi oct	0.37	-0.34	0.37	0.25	0.25	0.28	0.29	-0.43	-0.16	0.16	-0.47	0.45	0.25	0.18	0.32	-0.06	-0.33	-0.25	0.68	0.11	1.00	-0.04	-0.47	0.33
nitlit	0.00	0.02	0.00	-0.01	0.01	-0.01	0.01	0.00	0.02	-0.03	0.04	-0.04	-0.08	-0.04	-0.03	-0.01	0.12	0.01	-0.01	-0.03	-0.04	1.00	0.01	-0.04

ept	-0.58	0.76	-0.47	-0.20	-0.45	-0.28	-0.53	0.84	0.45	-0.47	0.11	-0.32	-0.28	-0.26	-0.43	-0.16	0.29	0.25	-0.68	0.44	-0.47	0.01	1.00	-0.55
rugg	0.18	-0.79	0.09	0.00	0.33	0.01	0.30	-0.62	-0.46	0.82	-0.20	0.23	0.40	0.35	0.39	0.12	-0.41	-0.17	0.37	-0.17	0.33	-0.04	-0.55	1.00

Abbreviations: aridity: aridity, Annual temperature: b1, Annual precipitation: b12, Rainfall of wettest month: b13, Precipitation of driest month: b14, Precipitation of wettest quarter: b16, Precipitation of driest quarter: b17, Maximum temperature of warmest month: b5, Minimum temperature of coldest month: b6, Elevation: dem, Distance from forest: df, Distance from grasslands: dg, Distance from cities: dnl, Distance from linear infrastructure: droad, Distance from water: dwat, Forest height: fh, Human pressure: hp, Livestock: lvsn, NDVI pre-monsoon: ndvi april, Deciduousness: ndvi diff, NDVI post-monsoon: ndvi oct, Night time light: nitlit, Evapotranspiration: ept, Ruggedness: rug

Appendix 3: Ecological observations based on which I formulated the hypotheses used for including/excluding covariates in modelling the occurence of invasive plants in the study. The abundance records from study area were overlaid on the forest cover map, climatic factors, human infrastructure, fire, livestock presence, etc. to arrive at the following conclusions.

Ageratina adinophora:

A herbaceous plant, with broad leaves and slender stem that was often recorded in the moist forests of lower Himalaya (e.g. Rajaji, Corbett), Terrai (e.g. Dudhwa, Valmiki), central moist deciduous forest (e.g. Similipal, Satkosia), Northeastern hills (e.g. Manas, Pakke), and Western Ghats (e.g. Periyar, Parambikulam). Within these forests it was observed around water channels, edges of the woodlands, high abundance along the roadside, grazing pastures and burnt forests. I hypothesize that its presence was determined by availability of water, canopy opening, human disturbance in form of linear infrastructure, agriculture, fire and grazing.

Ageratum conyzoides:

An erect herb observed in the grasslands, ridges, floodplains and open forests of lower Himalaya (e.g. Rajaji, Corbett), Terrai (e.g. Dudhwa, Pilibhit), central moist forest (e.g. Kanha, Satpura), Northeastern hills (e.g. Manas, Kaziranga), and Western Ghats (e.g. Mudumalai, Bandipur). Within these forests this species occurred abundantly in those open habitats that had higher moisture, frequently burnt, grazed or modified by humans. I hypothesize its occurrence to be determined by canopy opening, fire, human disturbance indices and soil moisture.

Chromolaena odorata:

This tall herb with broad leaves, profusely invaded wet forests in India with high occurrence in the Northeastern hills (e.g. Pakke, Manas) and Western Ghats (e.g. Periyar, Bhadra); but also was observed in moist parts of deciduous forests in central India (e.g. Melghat, Sahyadri). Within these forests it occurred inside the woodlands as well as along the grasslands, with high abundance in opn canopy, human settlement, roads and burnt areas. I hypothesize its occurrence to be determined by fire, canopy openness, wetness of the forest and human disturbance indices.

Hyptis suaveolens:

This herb was recorded mostly in the deciduous forests of central India (e.g. Melghat, Tadoba), with abundant presence on forest edges, roadside, nearby human habitation, water bodies and rugged terrains. I hypothesize its presence to be determined by moisture availability and canopy opening, with preference to human disturbed area like grazing pastures and proximity to roads and agriculture.

Lantana camara:

This woody shrub was sighted in all forest systems excluding the dry thorn forests in the western India, wet evergreen forest in Northeastern hills and Western Ghats. Its abundance was higher in all variations of forests and land-use. But mostly restricted by dense canopies in the Western Ghats, frost in Himalayan foothills, high temperature in semi-arid areas and management practices in the protected areas. Hence, I hypothesize its presence to be determined by climatic factors, canopy density of wet forests and proximity of human modified areas.

Mikania micrantha:

This herbaceous climber species was sighted in the wet forests of North East India (e.g. Manas, Nameri), Western Ghats (e.g. Periyar, Anamalai) and moist deciduous forests of Central India. Within these forests it abundantly occurred in grasslands, along the water channels, rugged areas and in proximity to human land use. I hypothesize its presence to be determined by precipitation parameters, canopy density, moisture content of soil and human disturbance indices.

Mimosa diplotricha:

This herb invaded the flood plains of Brahmaputra river and moist forest surrounding it. Its presence was also recorded in the Eastern Ghats of Odisha, Jharkhand and Chhattisgarh. Its presence coincided with grasslands, water logged areas, frequently burnt and human modified habitats, as well as forest along long roads and railways. I hypothesize its presence to be determined by water availability, fire frequency, canopy density and human infrastructure.

Parthenium hysterophorus:

This species occurred in the dry and moist deciduous forest systems across India (e.g. Bandipur, Amrabad, Navegaon Nagzira). Its abundance was high along the agricultural fields, grasslands, grazing pastures, savannahs and forest edges. I hypothesize its presence to be determined by open habitat, water availability in dry areas, frequently burnt areas, overgrazed areas and canopy openness.

Prosopis juliflora:

This woody shrub was spread across the drier parts of India. Its presence was abundantly found in the savannas and dry deciduous forests in the semi-arid parts of India including Rajasthan (e.g. Ranthambhore, Sariska), Gujarat (e.g. Gir), Central Maharashtra (e.g. Bor, Tipeshwar), Karnataka (e.g. Bandipur, Biligiri Ranganath Temple), Tamilnadu (e.g. Sathyamangalam) and Telangana (e.g. Kawal). Within these dry areas its abundance was determined by moisture availability hence I hypothesize its presence to be e a factor of water availability, suppressed fire regime, drier climate and proximity to human land use.

Senna tora:

This was amongst the most wide spread invasive plants in India. Its presence was found across all the forest systems and was limited by extreme hot condition in the Western deserts of India, prolonged frost in the Himalaya, saline water of the mangroves and water logged areas. I hypothesize its presence to be determined by climatic factors, proximity to human land use and canopy openings.

Xanthium strumarium:

This broad-leaf herb was mostly recorded in the central dry deciduous forests (e.g. Melghat, Tadoba, Pench) and savannas (e.g. Ranthambhore, Kuno). Its presence in these dry parts was mostly around the water bodies, roads and livestock trails. I hypothesize these factors in combination with drier climatic conditions to facilitate the invasion of this species.

Appendix 4: Estimates of naïve and modelled occupancy estimates of invasive plants in consistently sampled tropical forests of India. Values are forest areas in km².

Species	Naïve 2006	Modelled 2006	Naïve 2010	Modelled 2010	Naïve 2014	Modelled 2014
Ageratina adinophora	22,105	28467 (±2200)	24,590	31267 (±1402)	28,032	33418 (±1708)
Ageratum conyzoides	25,211	31678 (±3600)	26,446	35702 (±2421)	31,550	41579 (±1432)
Chromolaena odorata	37,934	40912 (±3590)	42,292	48924 (±2890)	51,891	58902 (±2550)
Hyptis suaveolens	9,658	11236 (±368)	10,584	13097 (±472)	13,549	14738 (±678)
Lantana camara	70,806	78932 (±4276)	73,221	80521 (±3562)	79,941	82003 (±3986)
Mikania micrantha	32,317	36490 (±1200)	43,547	44373 (±2355)	46,765	51829 (±3572)
Mimosa diplotricha	18,481	19029 (±1312)	19,003	21009 (±1769)	20,464	22190 (±1210)
Parthenium hysterophorus	39,565	41984 (±2145)	36,069	34023 (±1611)	35,784	35912 (±1437)
Prosopis juliflora	45,850	55945 (±3700)	49,211	61231 (±4210)	56,034	66753 (±2547)
Senna tora	65,380	73210 (±1194)	67,070	78012 (±1749)	70,111	82152 (±1180)
Xanthium strumarium	8,040	9879 (±734)	8,979	11632 (±1102)	9,564	12046 (±990)

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ORIGINAL PAPER

How global climate change and regional disturbance can expand the invasion risk? Case study of *Lantana camara* invasion in the Himalaya

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Abstract Presently, it is debated if regional conservation efforts can alone resolve the ecological problems that global climatic changes could bring. Biological invasion is one of such concerns. In the present study, we modeled how change in global climate and regional anthropogenic pressure can impact the distribution of invasive *Lantana camara* in the Upper Ganga valley of the Western Himalaya (India). The forest in the study area was stratified into 1 km^2 grid and two 15 m radius plot were located in each of the forest types in the grid, for recording Lantana presence. In total, 2221 plots were sampled covering 22% of forest. We used predictors representing the climate, forest patch size, fire and natural disaster variables for modeling the species distribution using maximum entropy algorithm. We further simulated 12 future landscape scenarios based on the global trends of these parameters. The present species—environment relationship was projected to these future landscape scenarios. Lantana was presently estimated to spread in 231 km^2 of the study area. It invaded larger forest patches in the subtropical region, and smaller disturbed forest patches in the warm and cold temperate region. Increased distribution of Lantana was projected across all the future scenarios. The study revealed how global climate changes and regional anthropogenic pressure can have a synergistic effect on the expansion of invasive species in the future. It thus questions the efficiency of conducting only regional efforts in absence of global initiative to reduce the greenhouse gases emission.

Keywords CCSM4 · MaxEnt · Range expansion · Species distribution model

Introduction

Given the unprecedented rate of global climate change and increasing anthropogenic pressures, it is increasingly important to understand how ecosystems and landscapes will adapt and respond to these drivers

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(MEA Board 2005; Tylianakis et al. 2008). One of the most significant drivers of change under changing climate and disturbance regimes is biological invasion (Vitousek et al. 1997) that leads to proliferation of non-native plants and animals in terms of distribution and displacement of native species. Invasive plants pose threats to native biodiversity and various ecosystem services worldwide (Pimentel et al. 2000; Hejda et al. 2009) and often exploit the chances provided by increasingly suitable climate and loss of native species due to disturbances like fire and increased road connectivity (Kuhman et al. 2010).

The impact of anthropogenic disturbance and changing climate varies for native and invasive plants and depends on their plasticity and/or dispersal potential (Hampe and Petit 2005). Plasticity to the changing climate and dispersal to new habitat depends on the evolutionary histories of plants and their habitats. For example, the floral composition of the Western Himalaya was found to have low colonization rate and elevation specific speciation, which resulted in autochthonous species assemblage in the higher Himalaya (Mani 1974). This long-term colonization and climate specific speciation makes the native plants incapable of surviving in the changed climate or long-distance dispersal to the new habitat. Whereas, for invasive plants of continental distributions, their physiological plasticity and strategies to earn new dispersal agents can benefit them by the global changes (Sharma et al. 2011). As a result, for those native plants which are highly adapted to changing disturbance regime, colonization of recently disturbed areas is likely (Kubisch and Fronhofer 2014). While for other less adaptable species local extinction might prevail (Aitken et al. 2008).

Lantana camara species complex (Lantana henceforth) is a shrub native to tropical Central and Southern America and recognized as an invasive species of concern in India (Bhagwat et al. 2012). Lantana has high phenotypic plasticity (Sharma et al. 2011) and genetic diversity (Ray and Quader 2014) and as a result it has established in over 60 tropical and subtropical countries (Parsons and Cuthbertson 2001). Since its introduction in the early nineteenth century in India for ornamental purposes, Lantana has invaded climatically diverse landscapes covering the tropical rainforest of Western Ghats (Sankaran et al. 2014), sub-tropical Himalayan Mountains (Dobhal et al. 2010), semi-arid landscape of the Western India (Bohra and Mishra 2012) and the mangroves (Panda et al. 2015). The distribution of Lantana is generally limited where winter temperature frequently falls below 5 °C resulting in defoliation and death of aerial woody branches (Day et al. 2003). Hence, the invasion range of Lantana is set by its physiological limits to the cold stress.

Lantana expands into new habitats following disturbances such as fires, landslides and floods, where native plants are stressed resulting from landscape degradation and fragmentation (Hiremath and Sundaram 2005; Raghubanshi and Tripathi 2009). Following disturbance, the forest canopy opens increasing the amount of light and freeing soil resources allowing the species to quickly colonize and invade. Lantana fruit attracts several bird species, which disperse its seeds far and wide (Sharma et al. 2005; Turner and Downey 2007). Moreover, the allelopathic characteristics of Lantana outcompetes the native plants and helps establish dense thickets (Gentle and Duggin 1997). Thus, changes in climatic conditions coupled with changes in disturbances regimes can act as drivers and significant predictors for future range expansion of Lantana.

Stakeholders are interested in understanding the current and likely future distribution of the species for prioritizing conservation efforts (Villemant et al. 2011). Species Distribution Models (SDMs) are often utilized as they provide a tool to predict the distribution quantitatively and spatially (Araújo and Peterson 2012). SDMs are useful for interpreting associated ecological interactions of a species and when utilized with spatially explicit climate and disturbance information can be used to better understand the geographic occurrence of the species and its environmental space. The global projection of the distribution of Lantana by 2050 differs depending on the analysis. A recent study predicted an increase in its distribution in response to climatic change alone (Qin et al. 2016), while another study found climatically suitable area to reduce in the future (Taylor et al. 2012). These studies suggest changes in the future range of the species but discrepancies in future projection are likely due to the different suitable habitat specifications and the role of disturbance in the simulations. It is crucial to understand how global climatic changes coupled with anthropogenic disturbance can influence the Lantana distribution in different parts of its range. In Himalaya, where Lantana is identified as high concern invasive plant (Mathur et al. 2015), its distribution is not known; as well as, relying on global scale estimate of its invasion level and future expansion can be erroneous for management decisions. Hence, it is essential to include climate, habitat attributes (e.g. forest patch size, flood, etc.), and anthropogenic disturbances that change landscape characters (e.g. fire and landslides) at microscale to derive its present and future distribution.

In this paper, we apply a SDM approach to model the current and future distribution of Lantana across the study area which represents the species' climatic range limit in Northern India and a global biodiversity hotspot. To do so, we first utilize spatial representations of climate, fire occurrence, evidence of past landslides and floods, and current native forest patch sizes to model the current distribution of Lantana. Second, we develop a series of future scenarios by projecting climate, fire, and forest patch size distribution under different assumptions of global and regional changes and investigate the subsequent impact on Lantana distribution. Finally, we utilize our research to identify forest patches that are vulnerable to Lantana invasion, and draw key recommendations for stakeholders based on the model simulations.

Methods

Study area

The study area lies in the catchment of Bhagirathi River in the Western Himalaya that extends from 30°07′N to 31°27′08″N and 78°08′29″E to 79°25′53″E covering 7644 km^2, in the state of Uttarakhand, India (Fig. 1). Winters in the area have become 1.5 °C warmer since 1982 and the summer precipitation has increased on average (Shrestha et al. 2012). The area is affected by climate change, which has retreated one of the biggest glacier (Gangotri) in the area (Kulkarni and Karyakarte 2014). These climatic changes are likely to influence the diverse array of vegetation types across various eco-climatic zones, viz., Tropical Moist Deciduous Forest (below 1500 m), Himalayan sub-tropical forests (elevation 1500–2000 m), Himalayan broadleaf forests (2000–2500 m), Himalayan conifer forest (2500–3000 m), Sub-alpine forest (3000–3600 m), moist alpine meadows (3600–5000 m) and alpine arid pastures or Desert Steppe (above 5000 m) (Rawat 2017). Currently, these categories are further divisible into various sub-classes and seral types (Champion and Seth 1968). Generally the forests at the foot-hills and warm temperate belts are much more extensive and less patchy as compared to higher altitudes owing to climatic and topographic features (Singh and Rawat 2012; Singh et al. 2016). However, most of south facing gentle slopes and wider river valleys (< 2000 m) have been taken over for human habitation and agriculture. Most of the communities inhabiting such areas depend heavily on extracting forest resources for subsistence. As a result, areas around human habitations are heavily fragmented (Tiwari and Singh 1987).

The forests in the study area have been influenced by anthropogenic activities including livestock grazing, extraction of non-timber forest products and fuel wood since several centuries (Awasthi et al. 2003; Rana et al. 2010). The increased anthropogenic pressures can be correlated with increased abundance of invasive plants in the area (Singh et al. 2016). In addition, frequent burning of hill slopes to increase grass growth by the local communities have changed vegetation structure and composition in the area (Mehta 1996; Gurumni 2000). Often accidental fires escape to the surrounding forests area resulting in the loss of forest cover. In the past decade on average 90 fire occurrences per year were recorded in the region. The area has also seen significant growth in human population and as a result landuse patterns in the valley have been shifted from smaller agro-pastoral forest mosaics to commercial landuses and homogenous agriculture farms (Raman and Punia 2012). Rapid infrastructure development including construction and widening of roads have led to excessive soil erosion and loss of catchment capability in the region (Haigh et al. 1995). As a result, the area has witnessed increased frequency of landslides and flash floods (Sati et al. 2011; Sati and Gahalaut 2013; Kala 2014), which has further fragmented the forests. Thus, the native forests in the study area are fragmented due to anthropogenic modifications in the landscape, which will likely continue in the future and have consequences on the native and invasive plants in the area.

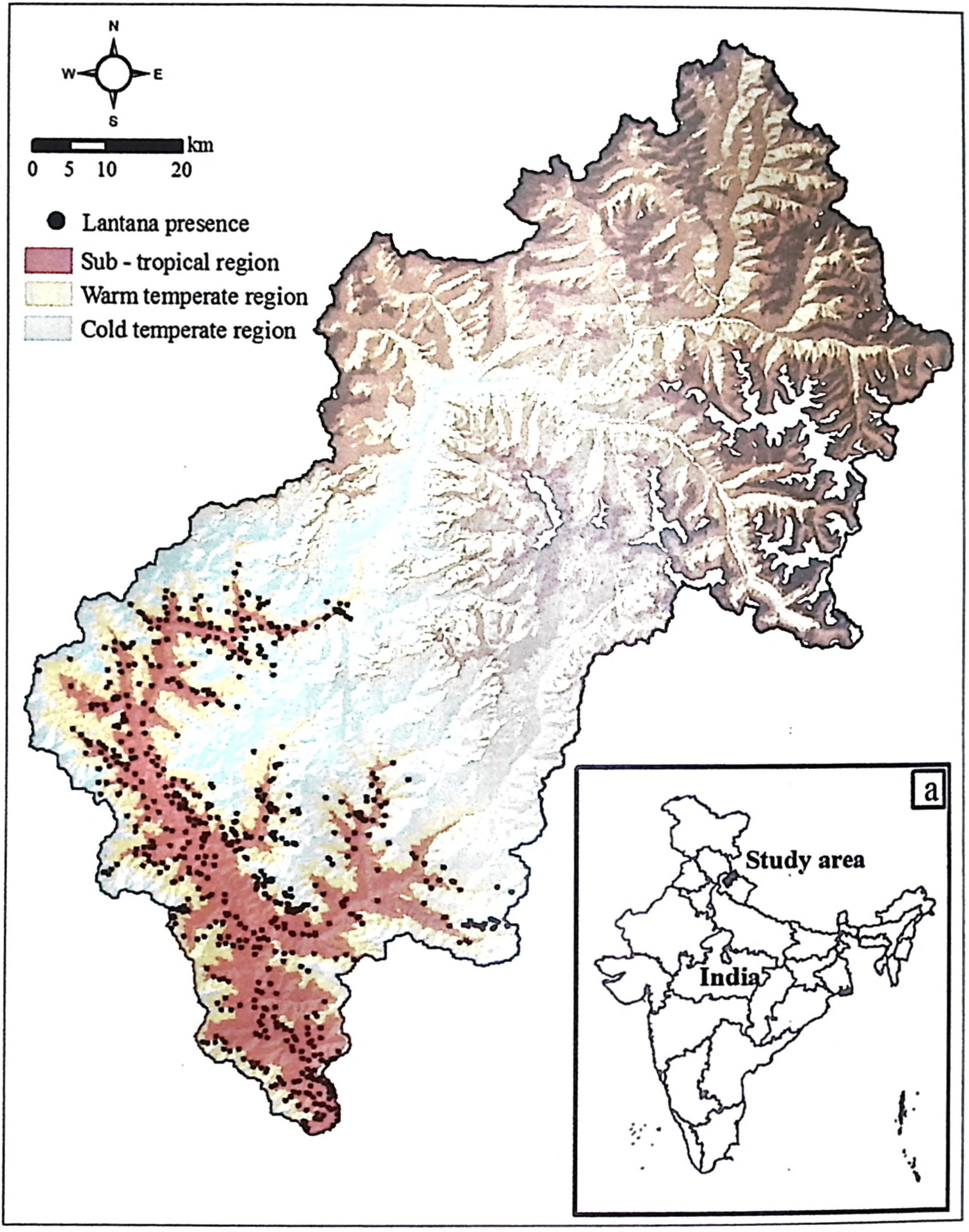

Fig. 1 Map depicting study area location in India (a) and Lantana presence in different climatic zones of the study area

Data collection

In order to explicitly model with behavior of Lantana across the very wide ecological environments in the study area we considered three ecological zones where it occurs: (1) Sub-tropical region (elevation < 1500 m) representing the lower warm valleys mainly dominated by *Shorea–Adina–Terminalia* deciduous broadleaf forest (Fig. 1, red color). (2) Warm temperate region (elevation 1500–2000 m) representing middle elevations that experience warmer summers as compared to the temperate area and cooler winters compared to sub-tropical area, mainly dominated by *Pinus roxburghii–Olea–Bauhinia* forest (Fig. 1, orange color). (3) Cold temperate region (elevation 2000–2500 m) which is the coldest area in the Lantana range and dominated by *Cedrus deodara* and other conifer forest (Fig. 1, blue color and the northern area beyond it).

Each zone was divided into a 1 × 1 km grid. Using an existing forest cover map (India state of forest report 2010) each grid was classified as either forested or non-forested. In each forested cell, two 15 m radius plots were randomly located separated by at least 200 m in each of the 16 forest types present in the grid. On an average, a cell had maximum of two dominant forest types and as a result between two to four plots were sampled in every cell of the grid. At each plot the presence of Lantana was visually assessed and recorded by a team of field biologists using a photographic field guide. Plots located in areas inaccessible due to difficult terrain were not sampled. During the sampling period of May–August 2016, 2221 plots were sampled in 802 grids, covering 22% (458 km^2) of targeted forests in the study area.

Predictor data

Climate

Lantana is limited by cold temperature in the study area and thus, minimum temperature of coldest month (b6) and mean temperature of coldest quarter (b11) was presumed important. Previous research (Qin et al. 2016) demonstrated b6 to be significant predictor of Lantana in addition to annual precipitation (b12), precipitation of the warmest quarter (b18) and precipitation of the driest month (b14); while maximum temperature of the warmest month (b5) and mean diurnal range (b2) contributed insignificantly. In the present study area, b14 and b18 are substantially similar and of less ecological significance, as most of the vegetation responds to annual precipitation (Mani 1974; Rawat 2017); and hence b12 was included as a predictor. Moreover, ground sampling revealed that Lantana was predominantly present in lower valleys, where the annual temperature (b1) and b5 were higher, and hence b1 and b5 were included as predictors. These climatic predictors were downloaded from Worldclim (www.worldclim.org) that provides climate data derived from different global and regional weather stations information compiled for 1950–2000 period (Hijmans et al. 2005). It is downscaled by using geographic and elevation information at 1 km resolution. We further downscaled the Worldclim variables to 30 m spatial resolution using the PRISM approach (Daly et al. 1997) that utilizes elevation and location information. A 30 m digital elevation model (DEM), obtained from the Shuttle Radar Topography Mission (SRTM), was resampled to 1 km to provide the required elevation data at the same resolution as the climatic data. Comparing climate to elevation revealed more than 95% variation in climate explained by elevation alone. The regression coefficients and intercepts were used to derive the climatic variables from 30 m DEM.

The same climate variables were obtained for 2050 conditions from the fifth Assessment Report of the International Panel of Climate Change (AR5, IPCC) (Stocker et al. 2013) for India. We used climatic scenarios for the four Representative Concentration Pathways (RCPs), which represent four greenhouse gas concentration scenarios based on the projection of human demographics and socio-economic conditions at end of this century (Moss et al. 2010). RCPs vary from the most optimistic scenario of reduced greenhouse gas emission after 2020 to the end of century, to the 'business as usual' scenario that assumes emission to increase with the present trend till 2100 (Van Vuuren et al. 2011). Every RCP results in climatic changes as shown in Table 1. The scenarios were developed under Community Climate System Model version 4 (CCSM4) released by the National Centre for Atmospheric Research (NCAR), which includes improvements in the treatment of clouds, aerosols, and land and sea surface temperatures (Gent et al. 2011). Downscaling of these climatic variables was also undertaken using 30 m DEM data and PRISM approaches.

Forest area

A forest type map showing the coverage of 16 forest types, derived from remotely sensed data and produced by the local state agency was available at 23.5 m scale and was resampled to a spatial resolution of 30 m for this study (India state of forest report 2010). The forest type map allowed individual forest patches to be mapped with a minimum mapping unit of 0.1 ha and patch area was subsequently used as predictor of Lantana distribution. In order to obtain future estimates of forest patch sizes across the study area we developed a climatic relationship between patch size, temperature and precipitation. Generally, every forest type has maximum patch size in the optimal climate, while at the trailing edge of the climatic range the stands get patchier and fragmented (Singh and Rawat 2012). Therefore, we modeled patch size at 30 m spatial resolution as a function of temperature and precipitation.

This relationship showed that across the study area, sub-tropical forest stands typically have larger patch sizes in humid-warm areas and more fragmented as

Table 1 Projected future scenarios by combining four global greenhouse gas emission scenes, which vary from the most optimistic reduced emission (RCP 2.5) to business as usual scene (RCP 8.5); with change in forest area and fire occurrences

Future scenario	RCP 2.5	RCP 4.5	RCP 6	RCP 8.5
Change in climate	Scenario 1 (1 °C rise in the temperature, active forest restoration and fire prevention)	Scenario 2 (1.4 °C rise in the temperature, active forest restoration and fire prevention)	Scenario 3 (1.3 °C rise in the temperature, active forest restoration and fire prevention)	Scenario 4 (2 °C rise in the temperature, active forest restoration and fire prevention)
Change in climate and forest area	Scenario 5 (1 °C rise in the temperature, forest area reduced by 426 km^2 and fire prevention)	Scenario 6 (1.4 °C rise in the temperature, forest area reduced by 427 km^2 and fire prevention)	Scenario 7 (1.3 °C rise in the temperature, forest area reduced by 866 km^2 and fire prevention)	Scenario 8 (2 °C rise in the temperature, forest area reduced by 874 km^2 and fire prevention)
Change in climate, forest area and fire	Scenario 9 (1 °C rise in the temperature, forest area reduced by 426 km^2 and fire frequency reduced by half of present)	Scenario 10 (1.4 °C rise in the temperature, forest area reduced by 427 km^2 and fire frequency similar to present)	Scenario 11 (1.3 °C rise in the temperature, forest area reduced by 866 km^2 and fire frequency increased threefolds of the present)	Scenario 12 (2 °C rise in the temperature, forest area reduced by 874 km^2 and fire frequency increased by fivefolds of the present)

climate gets colder. Temperate forest gets more fragmented as the climate gets dry-hotter or dry-cold (Rawat 2017). With future change in the climate regime, the distribution of forest patch distribution is likely to change. We used maximum temperature of hottest month, minimum temperature of coldest month and range of rainfall in a particular forest type to define its climatic range. Under climatic change, the range of each forest type will change; beyond which the native plants of that forest type will likely suffer heat stress or cold stress resulting in fragmentation and reduction of patch area (Allen et al. 2010; Kulakowski et al. 2011). Thus, we derived the climatic ranges of different forest type under each RCP and assigned the least forest area to the patches that fall out of the shifted climatic range. This adjusted forest areas for every RCP was used as scenario of future forest patch distribution for modeling future distribution of Lantana.

Landslides and flood affected areas

We derived disturbance due to landslides and flood areas from the 30 m SRTM data using slope length (LS factor) and the Topographic Wetness Index (TWI). LS factor is an index that considers steepness of a slope and its length of relative soil loss to derive the potential of soil erosion (Lee 2004). These identified areas also represent the sites that mostly undergo different magnitudes of landslides (Poudyal et al. 2010). TWI quantifies the effect of topography on runoff generation and predicts the area subjected to overland flow i.e. floods (Beven and Kirkby 1979). Higher TWI values represent converging valleys or flat terrain that has high potential of water saturation (Schmidt and Persson 2003). We cross-validated the derived potential landslide and flood areas with landslide and flood occurrence data in the past five years based on observed disturbance events and observations. In total, 56 landslides and 33 flooded sites were recorded in the study area. We cross validated the derived indices by assessing the predictions for actual locations of an event, when TWI > 15 and LS factor > 5 was considered as occurrence of an event. We assume that in 2050, excluding major topographic changes (such as earthquakes), landslide and flood areas will not change. Hence, the LS factor and TWI were kept constant for present and future projections.

Fire

We obtained information on fire occurrence from the Fire Information for Resource Management System (FIRMS) database, which consisted of daily MODIS hotspots and Visible Infrared Imaging Radiometer Suite (VIIRS). The MODIS active fire product detects fires at 1 km resolution through middle—infrared and thermal infrared brightness temperature (Giglio et al. 2003). VIIRS detects fire at 375 m resolution using multispectral bands and complements MODIS for detecting fires of smaller extent (Schroeder et al. 2014). In total 1424 Fire occurrences that were larger than 375 m were recorded for the period of 2000–2016 in the study area. The majority (1173) of the fires were located around the lower valley i.e. in sub-tropical and warm temperate region, which had more human settlement compared to cold temperate. We used distance from the fire as a predictor of Lantana, as fire can burn nearby area or degrade it by spreading ashes and smoke that can support Lantana invasion (Hiremath and Sundaram 2005).

Climate change is likely to increase the natural fire frequency, which coupled with increased population will elevate the chances of fire. For projecting future fires, we used global fire projections (de Groot et al. 2013) and socio-economic assumptions of different RCPs. To do so, we calculated per year fire incidence (fire frequency) in different forest types since 2000–2016. Under RCP 2.6, we assumed the optimistic condition in socio-economic criteria, where the fire frequency is reduced by half due to preventative actions of concerned stakeholders and public awareness. Under RCP 4.5, we assumed that the fire frequency was stable. Under RCP 6.0, we used the global prediction of increase in the fire frequency by three folds, and under RCP 8.5 by fivefolds. The total number of deduced fire occurrences was simulated in every forest type and Euclidian distance from it was used for SDM.

Apart from the considered environmental covariates, Lantana is likely influenced by the edaphic parameters in the study area. Himalaya being predominantly metamorphic and sedimentary rock, has complex soil structure. Absence of soil data at desired scale or its future projections, restricted us to exclude soil parameters from the present study.

Species distribution modeling

We used the Maximum Entropy (MaxEnt) (Phillips et al. 2006) approach for modeling Lantana distribution under present and future scenarios. MaxEnt has been successful in accurately modeling the distribution and forecasting similar invasive species (Pawar et al. 2007; Roger et al. 2015; Adhikari et al. 2015; Choudhury et al. 2016; Qin et al. 2016). The field dataset was divided in 80% of the data used for model development, and 20% used for testing.

Four model types in MaxEnt were tested (linear, quadratic, hinge, and threshold) with the model cross-validated using a 25% test sample drawn randomly from the presence locations. As the presence data was systematically surveyed throughout the region and the species was homogenously present, drawing random background points within the same climatic region was the most valid option (Phillips et al. 2009; Elith et al. 2010). In order to increase the number of absent cells we used 10,000 background points randomly drawn from within the region. 100 bootstrap resampling runs were performed and the mean logistic probability and AUC score (Area Under Curve) of the receiver operation characteristic (ROC) was reported for enhancing the modeling precision (Peterson et al. 2008). We used jackknifing for assessing the relative contribution of each variable on species presence. The regularization function was adjusted to 1, as the model it produced was visually most accurate (Elith et al. 2010). MaxEnt output for every scenario was converted into presence distribution based on the 10th percentile presence threshold (Radosavljevic and Anderson 2014). This model established the relation of Lantana to the environment and estimated its distribution in the study area.

Accuracy assessment of the model was undertaken using the 20% testing data not used in model development. For providing an overall assessment, we used the kappa statistics as it is a conservative measure of agreement when the classes to test are only two (Uebersax 1987).

Twelve future scenarios were developed based on a range of climatic, fire and forest patch scenarios discussed earlier. Under the four climatic scenarios we developed a set of scenarios based on fire and patch size distribution, stable fire yet decreased forest patch distribution set and an increasing fire and decreasing forest patch distribution (Table 1). The present species-environment relationship was used in each scenario as a comparison control. With these projections MaxEnt also estimated the effect of clamping (effect of covariate values beyond the range in the training data) on the output (Elith et al. 2010). We removed all the pixels where the clamping was more than 0.8. This produced the projected area of Lantana for different future scenarios of the landscape.

All the analysis was done using R (ver 3.0.3), SAGA GIS and Arc GIS 10.2.

Result

From the field observations, Lantana was recorded in 1109/2221 plots, yielding naïve occupancy of 50%. Its invasion was recorded in six forest types: Moist Siwalik Sal forest, Northern dry mixed deciduous forest, Upper or Himalayan Chir Pine forest, Himalayan sub-tropical scrub, *Quercus leucotrichophora* forest and West Himalayan upper Oak/Fir forest. Hence, all scenarios were focused on these forest types. The highest elevation which had Lantana presence was 2112 m, whereas the minimum winter temperature of a plot with presence of Lantana was 5.6 °C. This plot was near the human settlement, where the forest was frequently burnt for fodder production. Lantana was not detected in plots (n = 69) geographically above this point. The LS factor and TWI could classify 96 and 92% of the landslide and flooded sites in the study area, indicating agreement to accurately index the landslide and flooded sites.

Forest patch size was found to be the most significant predictor of Lantana distribution through MaxEnt, where its invasion decreased with increase in patch size. Other covariates and their permutation importance to predict Lantana in the study area and their Jacknife test are depicted Table 2. In the sub-tropical area, Lantana was predicted to expand into colder and hotter areas (lower and higher mean winter temperature), which are dry (low annual precipitation) and recently disturbed landslide sites away from fire. In warm temperate area, Lantana was predicted to expand into colder areas (low mean winter temperature), with less rainfall but near to the disturbed patches (fire, landslide and flood). In cold temperate area, the species preferentially was predicted to occur in hot (high mean winter temperature), humid (high annual precipitation) areas that are frequently burnt, but not disturbed by landslide or flood area (stable substrate). Differences in the predicted occurrence in relation to forest patch size, winter temperature and fire in three regions is depicted in Fig. 2. We selected these variables as they significantly differ in the response across its distribution, and provide insight into its ecology.

The potential area invaded by Lantana in the valley was 231 km^2; out of which 217 km^2 was sub-tropical region, 11 km^2 was warm temperate region and 4 km^2 was cold temperate region (Fig. 3). The probability map of Lantana distribution is provided in Online Resource 1. The accuracy assessment under current conditions, using the 20% (n = 222) of the test data not used in model developed, resulted in kappa statistics of 0.86, 0.94 and 0.98 for sub-tropical, warm temperate and cold temperate area respectively. The area under the receiver operating curve (AUC) for the distribution models were 0.70 (± 0.09), 0.90 (± 0.05) and 0.94 (± 0.04) respectively. This suggests that MaxEnt has modeled Lantana invasion accurately for the study area (Elith et al. 2011).

The assumed fire occurrences in different forest types under future scenarios are given in Table 3. The projected distribution of Lantana against 12 future scenarios based on global and regional assumption

Table 2 Contribution of different environmental covariates to MaxEnt model of Lantana in sub-tropical, warm temperate and cold temperate regions of study area

Variable	Sub-tropics (% contribution)	Warm temperate (% contribution)	Cold temperate (% contribution)
Forest patch size	79.7	98.8	89.6
Mean winter temperature	14.1	0.2	2.5
Elevation	2	0	0.5
Distance from fire	3.2	0.5	0.1
Annual precipitation	0.2	0.2	5
Flood index	0	0	1.8
Landslide index	0.8	0.4	0.5

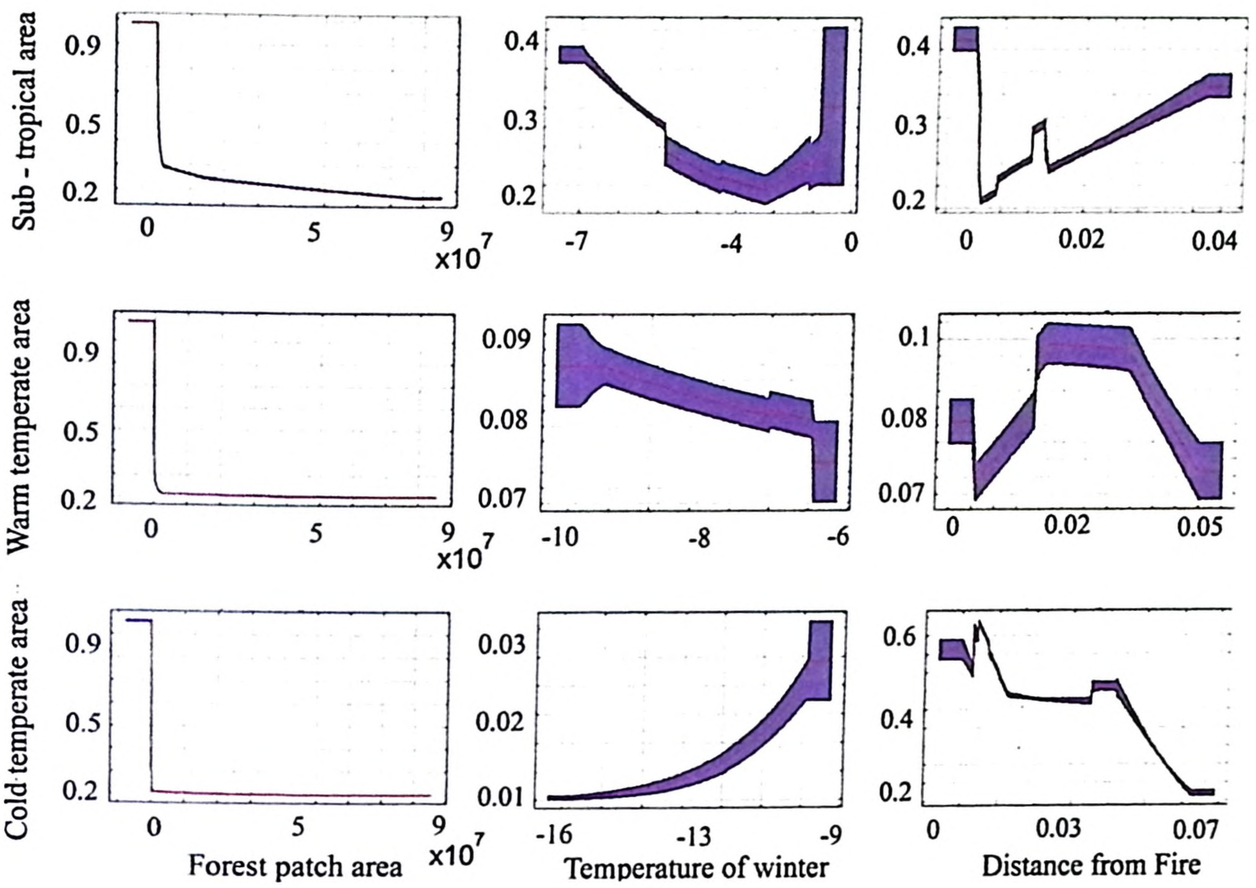

Fig. 2 Graphs depicting probability (± SD) of Lantana occurrence as a response to forest patch size, temperature of winter and distance from fire in sub-tropical, warm temperate and cold temperate regions of the study area. In sub-tropical region, Lantana invaded moderately sized forest patches, decreased with higher winter temperature and was present around as well as away from fire occurrence. In warm temperate region, Lantana invaded small forest patches, decreased moderately with increase in winter temperature and was present in proximity to fire occurrences. In cold temperate region, Lantana invaded smaller forest patches, increased with temperature of winters and fire occurrence

(Fig. 4) is shown in Table 4. The largest expansion in Lantana invasion range was up to 375 km^2 under scenario 4. The most conservative estimate given was 317 km^2, under scenario 3. Thus, the projected relationship to the future scenario revealed that Lantana will expand its distribution under a decrease in sustainability (increased emission) of the landscape. In addition, where the regional changes are actively managed by restoring forest area and preventing fire, the invasion range will expand due to global climatic changes. Forest patches vulnerable to Lantana invasion under each scenario are shown in Fig. 5.

Discussion

The results of this study provide managers with information on the present and future distribution of Lantana under changing regional disturbances and global climate change. Our study estimates that 94% of total Lantana distribution is recorded in the sub-tropical region of the valley, which provides an optimal climatic environment for this tropical shrub. We found that the Lantana distribution decreased with increases in elevation and decreases in temperature, with the species distribution broadly limited by a mean winter temperature of less than 5.5 °C. Our results also indicate that native forest patch area was significantly negatively related to the Lantana distribution, with the influence of forest patch size more important at the edges of the species climatic range. Response of Lantana to these environmental parameters also affirms our apriori hypothesis of climatic extremities and anthropogenic disturbance explaining majority of Lantana invasion.

Despite the marked forest fragmentation in the sub-tropical portion of the study area, Lantana invaded larger forest patches away from disturbance events like fire and floods. This could be attributed to the favorable climatic conditions due to which resource utilization and competitive abilities (allelopathy, etc.) can be maximized. However, its distribution also increased with landslides in the area, which can be attributed to the construction of new roadways. In the warm temperate region, where the summer temperature is similar to the tropical region but winters are

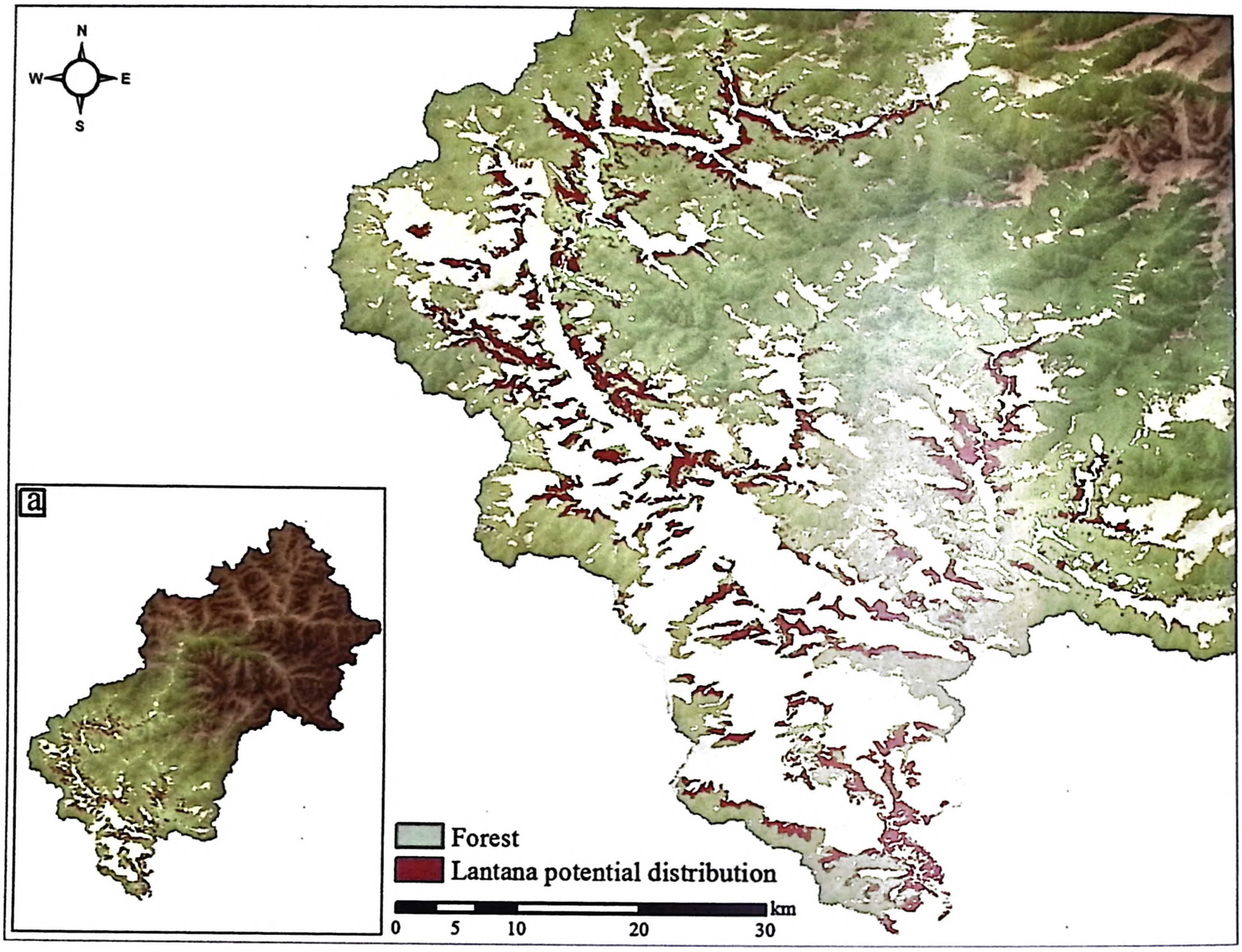

Fig. 3 Range of Lantana invasion in the study area (a) and its potential distribution in the forest

Table 3 Projected fire occurrence under the future scenario where the fire frequency is halved (RCP 2.5), unchanged (RCP 4.5), increased by threefolds (RCP 6.0) and increased by fivefolds (RCP 8.5) from the present fire frequency in different forest types

Forest type	RCP 2.5	RCP 4.5	RCP 6.0	RCP 8.5
Quercus incana forest	478	984	1350	2250
West Himalayan upper Oak/Fir forest	34	70	96	160
Moist Siwalik Sal forest	7	15	21	35
Himalayan Chir Pine forest	383	788	1080	1800
Himalayan sub-tropical scrub	30	61	84	140

colder, Lantana invaded small forest patches. In this region, the species occurred at a distance from fire disturbance yet closer to landslides and flood sites. However, in the cold temperate region, where Lantana distribution is chiefly constrained by the cold temperature, it occurred in warmer areas with higher rainfall and stable substrate (away from landslides and floods). It invaded smaller forest patches that were burnt, which provides a niche opening with unutilized resources and minimum competition. Thus, climate, forest fragmentation and anthropogenic disturbances are significant predictors of Lantana presence that can

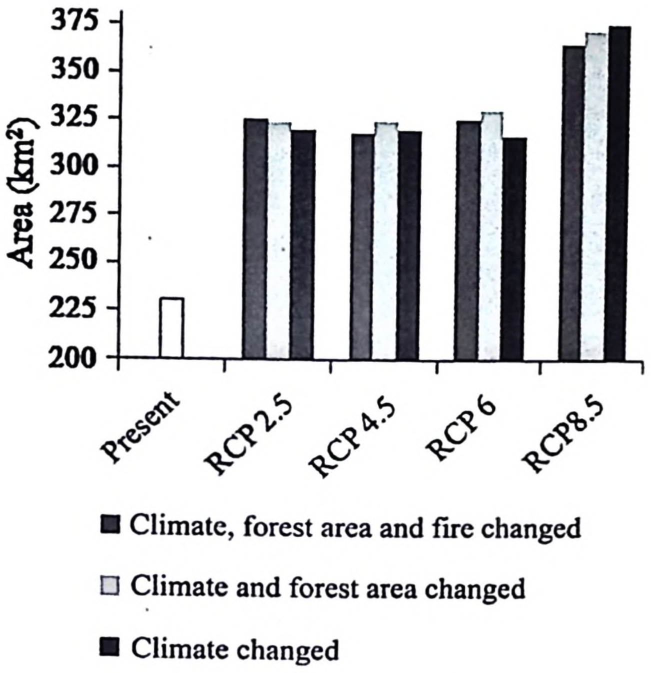

Fig. 4 Area invaded by Lantana under present and future environmental scenarios

substantially influence its future distribution and range expansion.

The future impacts of global climatic and regional anthropogenic changes were simulated in 12 different scenarios, which revealed differential increases in the distribution of the species throughout the valley. The projected greatest distribution area was solely due to changes in global climatic variables (scenario 4), despite regional efforts of forest restoration and fire prevention. However, a consistent increase in the area of Lantana distribution was projected by all the scenarios (scenario 5, 6, 7 and 8) that considered climatic change coupled with regional forest area loss/fragmentation. The second consistent increase in species distribution was projected by all the scenarios (scenario 9, 10, 11 and 12) that considered climate and forest changes with addition of fire. The 'worst-climate' as projected under scenario 4 leaves no space for improvement or sustainability; and is globally prevented by making different emission regulation policies. The intermediate scenarios that are outcome of conservative climatic changes reduced the area of the distribution with increased forest restoration and fire prevention. The result of this study contradicts the global projection of Lantana distribution in the future (Taylor et al. 2012) and supports the increased invasion hypothesis (Qin et al. 2016).

Lantana's future distribution is likely to be influenced by interaction of the considered covariates or additional factors not considered in this research. At the micro scale, the species is likely impacted by soil nutrient dynamics that are projected to change in the future (Clair and Lynch 2010) and community composition (Lavergne et al. 2010). Incorporating these processes into mechanistic models would be an improvement on the present correlative models, which only address effects of changes in environmental variables (Kearney and Porter 2009). These environmental future projections can have further issues due to assumptions of General Circulation Model (GCM)

Table 4 Projected Lantana invaded area under future environmental scenarios

	Area invaded by Lantana (km²)			
Future scenario	RCP 2.5	RCP 4.5	RCP 6	RCP8.5
Change in climate	Scenario 1:	Scenario 2:	Scenario 3:	Scenario 4:
	320	320	317	375
Change in climate and	Scenario 5:	Scenario 6:	Scenario 7:	Scenario 8:
forest area	324	324	330	372
Change in climate, forest	Scenario 9:	Scenario 10:	Scenario 11:	Scenario 12:
area and fire	326	318	325	365

Darkest color represents highest change

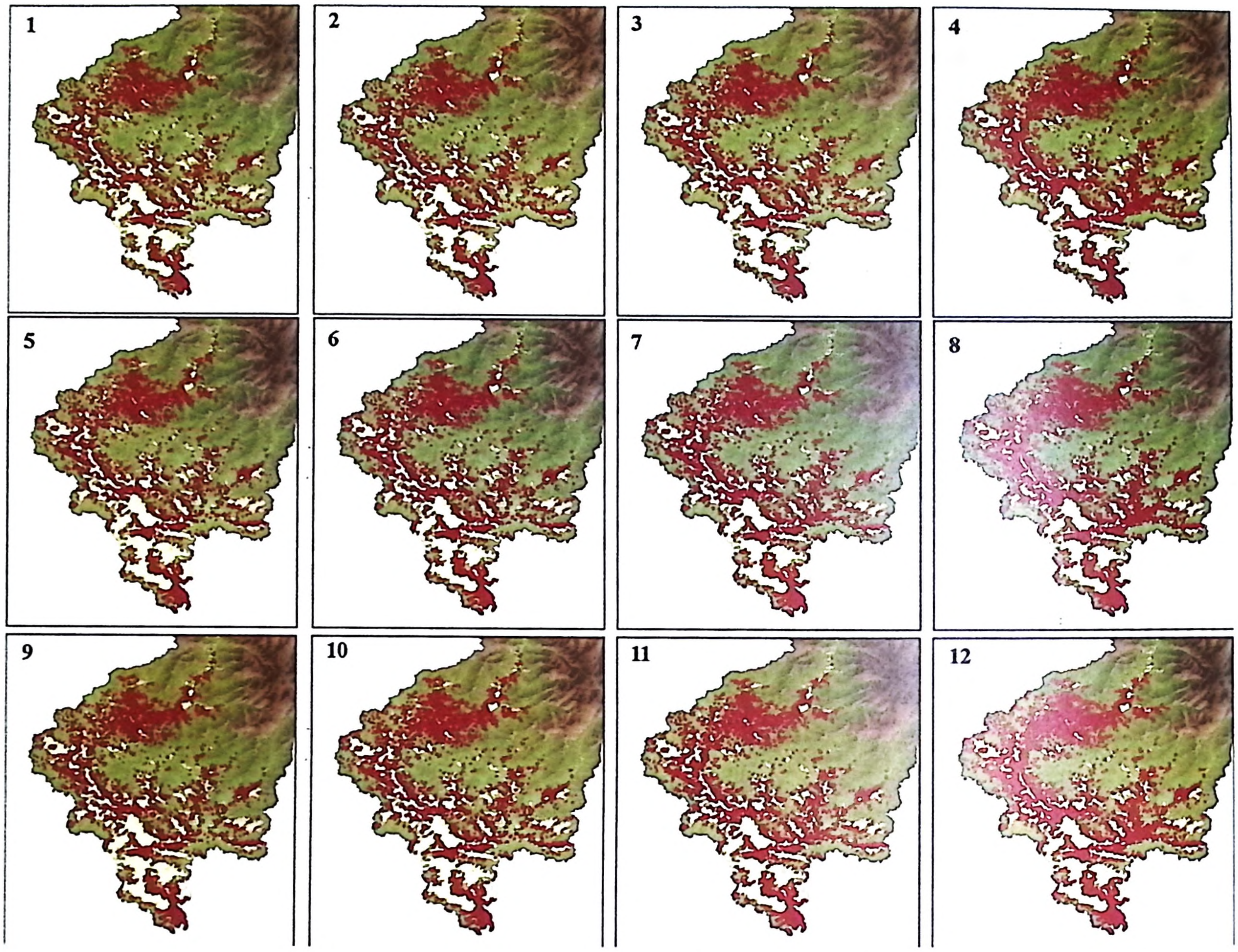

Fig. 5 Projected distribution of Lantana in the study area under different future environmental scenarios. Map number depicts the scenario number

used in the study, which is based on the global conditions that may differ from the study area conditions; and hence caution should be made while interpreting results based on such models.

This climate-disturbance induced invasion can form a positive feedback loop in which invasive species exert a competitive pressure on the native plants and degrade the forest patches which further helps invasion (Didham et al. 2005). Native tree species in the valley, which are affected by the climatic changes and human extractions (e.g. *Quercus leucotrichophora, Cedrus deodara*) can become further vulnerable to Lantana invasion (Tiwari and Singh 1987; Singh et al. 2016). This will impact the ecosystem services like soil moisture, fuel wood, carbon regularization and habitat for many species in the valley (Rana et al. 2010). Study results shows fire to be the important factor in facilitating Lantana invasion in cold temperate areas. Thus, we suggest that minimizing fire frequencies in cold temperate can potentially control the future invasion of Lantana in these forests. The study can be used to identify the forest patches that are currently invaded by Lantana and require active managerial actions to eradicate the species. We also identify forest patches that are vulnerable to Lantana invasion in the future, these forest patches should be monitored for any colonization evidence of Lantana. Any seedling and sapling of Lantana in these patches should be removed to avoid the future expansion of species. It indicates the necessity of continuous monitoring of the landscape by combining remote sensing and ecological surveys.

The future projection also revealed that regional actions for mitigating the increased invasion may not be adequate as the majority of the range expansion occurs as a response to change in global climatic scenarios. As recent global climatic changes are manifestation of human induced local disturbances, adopting a proactive control measures for such disturbances in place of reactive mitigation measures is globally needed to sustain the ecological integrity and allied services. Thus, more policy actions are needed at the global scale for reduction in the greenhouse gasses emission to avoid similar range expansion and collapse of native ecological communities worldwide.

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Original Research Article

Expanding niche and degrading forests: Key to the successful global invasion of *Lantana camara* (sensu lato)

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ABSTRACT

Estimating the distribution of invasive species and understanding the ecological reasons for their success is crucial for their management. Moreover, their ability to invade biogeographically distinct regions in short timespans poses interesting ecological questions. *Lantana camara* (sensu lato) is one such invasive species of global concern. In an unprecedented effort, we surveyed 207,100 km^2 of Indian forests by sampling 13715 grids of 5 × 5 km, each with 1–31 plots of 10 m diameter, to record the abundance of Lantana. For India, we modeled occupancy of Lantana in the sampled area by accounting for imperfect detection; and potential invasion outside the sampled area using MaxEnt with covariates of climate, soil, forest and human disturbance. Further, Lantana's response in comparable areas of its native and global invaded range was modeled using MaxEnt to provide a better understanding of its changing relationship with environmental factors. Lantana invaded 154,837 km^2 of the surveyed area, and threatened 303,607 km^2 of total Indian forests (44%); with preference to warm, humid, fertile areas, degraded by extractive human use. By combining our large-scale ground surveys with published data, we show that Lantana has expanded its climatic niche worldwide, with >11 million km^2 suitable for its invasion. Niche comparison revealed that Lantana might have adaptive plasticity in its invaded range; where it was found to be more tolerant to higher temperatures, lower fertility and shade as compared to its native range. In light of Lantana's introduction history that suggest excessive hybridization between previously allopatric populations, and its known genetic diversity in the invaded range, the existing adaptive plasticity is suggestive of contemporary evolution. This adaptive nature can increase area under its invasion and pose an ecological conundrum of managing an evolving neophyte.

1. Introduction

A few decades ago, many scientists speculated that the introduction of invasive species by humans could be one of the top threats to the global biodiversity (Elton, 1958; Diamond, 1989; Sala, 2000). Recent global studies validated these speculations by showing homogenization of global biota and increased extinction of native species catalyzed by biological invasions (Simberloff et al., 2013; Bellard et al., 2016; IPBES, 2019). Biological invasions have caused an enormous economic loss by

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affecting livelihoods, human health and ecological integrity of the invaded areas (Pimentel et al., 2001). With increased global connectivity, the chances of introducing potentially invasive species have increased, particularly in developing countries that have higher demand for international goods exchange and poor quarantine policies (Meyerson and Mooney, 2007). Additionally, over extraction of natural resources for livelihood in developing countries has degraded their native ecosystems, making them vulnerable to biological invasions (Byers, 2002).

Amongst invasive plants, *Lantana camara* L. (sensu lato) (Goyal and Sharma, 2015) (hereafter Lantana), a woody shrub of tropical American origin (Fig. 1), is regarded as one of the ten worst invasive species in the world (Ghisalberti, 2000; Richardson and Rejmánek, 2011) and a major concern in India (Mungi et al. 2018). Previous studies found multiple species and varieties of Lantana introduced during the 1800s across the tropics where it was introduced. These species and varieties were introduced as hedge plants and were subsequently hybridized for improved stand and other ornamental properties (Kannan et al., 2013). This potential hybridization added to the number of varieties, which were later reported to invade native forests (Bhagwat et al., 2012). What is now identified as '*Lantana camara*' in its invaded range is thus a hybrid of many species/varieties. This hybrid is caused by multiple sources of introductions, artificial selection and subsequent escape into natural systems to express the altered phenotype (Ray and Ray, 2014). As a consequence, recent studies have categorically identified this group of Lantana as '*Lantana camara* (sensu lato)' (e.g. Goyal and Sharma, 2015). Dense invasion of Lantana has been suspected of causing a decline in wildlife habitat and native plants (Aravind et al., 2010; Wilson et al., 2013). Lantana has also affected the livelihood of communities dependent on forest resources (Sundaram and Hiremath, 2012). Its management is estimated to cost around $18,700 per km^2 in India (Babu et al., 2009). A prerequisite to tackling macro-ecological concerns like biological invasions is at first a reliable assessment of state variables such as occurrence and abundance of species at landscape scales (Hastings et al., 2005). Despite 200 years of managing Lantana in India (Bhagwat et al., 2012), little information regarding its distribution at the country level or its biogeographic correlates is available. Published literature on these aspects rely on the potential distribution of Lantana derived through climatic niche modelling and suffers due to data deficiency (Panda et al. 2018).

An understanding of mechanisms that enable or restrict invasion would be useful in designing control mechanisms. These mechanisms can be evaluated by comparing the niche within native and invaded ranges of an invasive species (Peterson et al., 2006). For a valid comparison, it is essential that models used for explaining a species' niche be within the same ecological space (analogous areas) used for training and prediction (Barve et al., 2011). Often this basic assumption of statistical modelling is violated, making the inferences questionable (Araujo and Guisan, 2006; Rodda et al., 2011; Qiao et al., 2017). To assess and demonstrate niche expansion in an invaded range, comparison of niche space should be limited to analogous areas in the native and invaded range (Peterson, 2011). However, this limitation of comparing only analogous areas, is often overlooked by many studies that demonstrate niche expansion (e.g. Rödder and Lötters, 2009; Di Febbraro et al., 2013). Therefore, inferences from such studies cannot differentiate between actual change in the niche space in invaded area or the species' inability to express its full niche potential due to the unavailability of niche space in its native or introduced range.

Though climatic niche change in analogous areas is often used as a proxy for fundamental niche change, changes estimated from non-analogous areas can be used as a proxy for realized niche change (Escobar et al., 2016). Unlike the climatic niche expansion, which hints at physiological adaptations in a species, realized niche change provide a unique natural experiment to disentangle the biogeographic responses of the species when freed from natural controlling agents like competitors, predators and diseases. Hence, increasing number of studies include an influence of biotic parameters in understanding niche changes (Tingley et al., 2014). Changes in realized niche also explain how different disturbance regimes and facilitating agents influence the spread of invasive species, thus providing insights for their management. As an example, Lantana distribution is known to be influenced by native forest fragmentation in invaded areas (Mungi et al., 2018).

Ravindranath et al. (2012) estimated forest loss in India at a rate of 173 (±39) km^2/year, which is lower than many other tropical countries (www.globalforestwatch.org). While forest loss is restricted to loss in the tree cover, changes in grasslands

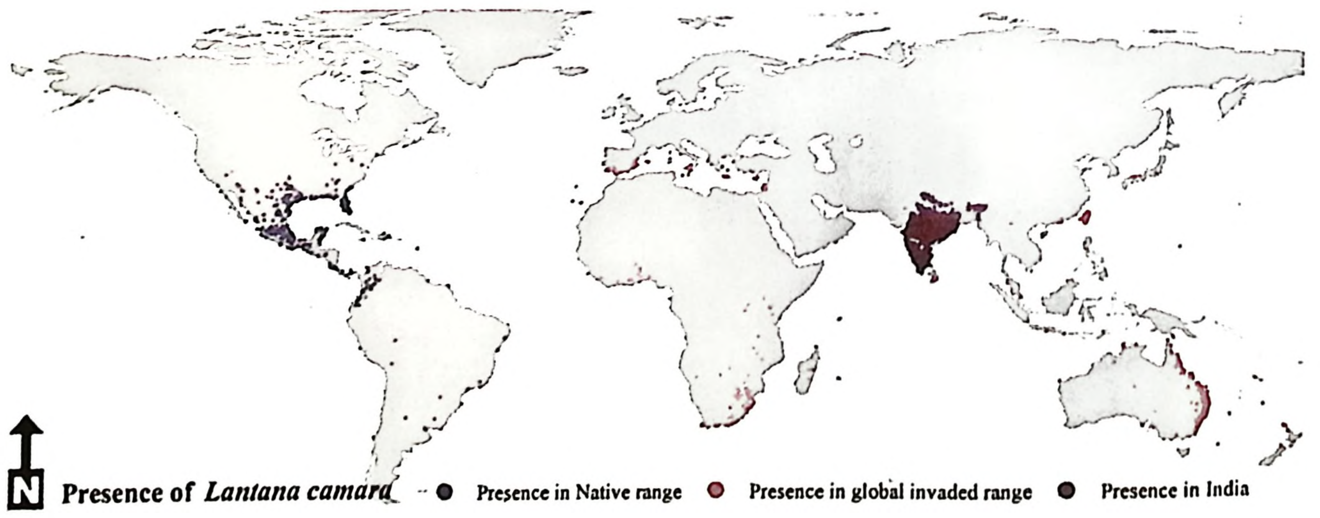

Fig. 1. *Lantana camara* presence locations from its native range in tropical America (blue), and invaded range (GBIF data (orange) and field sampling based data from India (maroon)) used in the study.

and savannas are more insidious and undocumented (Ratnam et al., 2016). These modifications of vegetation are known to facilitate the invasion of many plants, including Lantana (Gudiel et al., 2016). However, most often the conversion of native vegetation into invaded vegetation is neither reported as forest loss, nor is it quantified. As a consequence, government policies compensate forest loss by compensatory afforestation or similar measures, while the management of invasive plants and restoration of native vegetation remains unattended. Secondly, the facilitation of invasion by degradation of forest, though significant, is often overlooked. Forests in tropical developing countries, including India, are used by people for their livelihood (e.g. timber extraction, forage extraction, etc.). These unsustainable extractive dependencies can degrade quality of the native vegetation community (Raghubanshi and Tripathi, 2009). It is hence, essential to quantify and understand the effect of forest loss and degradation on biological invasions so as to prioritize the conservation investment.

We address lacunae in invasive species management by providing evidence of how forest degradation is influencing the Lantana invasion in India. In the current study, we use data from one of the largest and the most extensive sampling efforts undertaken for any invasive species to develop an accurate countrywide map of Lantana invasion for informed conservation actions. By combining this information with globally available presence information of Lantana, we investigate the environmental factors that facilitate Lantana invasion globally and India in particular. We provide a reliable estimate of the potential global range of Lantana invasion. We interpret our results in the light of phenotypic plasticity of Lantana and its implications in the era of climate change and forest degradation.

2. Materials and methods

2.1. Sampling and data sources

We generated a spatial grid of 5*5 km for India in ArcGIS 10.6.1. Our study was limited to forested areas, therefore we computed the area under forest within each grid. For this, we used the forest cover map from Survey of India (Indian State of Forest 2013), wherein the categories of scrub land, open forest, moderately dense forest, and dense forest were combined as 'forests'. We sampled forested grids in 18 Indian states by laying 1 to 5 transects of 2 km length in each of these grids. On these transects, at every 400 m nested circular plots of 30 m for human disturbance and 10 m for shrub species were sampled. Shrub cover (including Lantana) was scored into four categories using a modification of Daubenmire's scale (1968) (absent, low abundance < 10% of groundcover, moderate abundance 10–50% of groundcover, and high abundance > 50% of ground cover) (Jhala et al., 2010). Lantana invasion is known to be facilitated by human disturbances and perturbation of the ecosystem (Hiremath and Sundaram, 2010; Mungi et al., 2018). We therefore collected data in every 30 m diameter plot on a) the number of trees lopped, b) the number of trees cut, c) evidence of grass and bamboo cutting (as present or absent), d) number of people seen from the plot, and e) number of livestock seen from the plot and f) number of livestock-human foot trails within the plot. A forest guard, who is the front-line staff of the forest administration across the country and has an intimate knowledge of the forest, participated as a team member for sampling these plots. The survey path and plot locations were recorded using a handheld GPS unit (Garmin Etrex model 72). The sampling was conducted between November 2009 and March 2010. In total 117,104 plots were sampled (Fig. 1) within 13,715 grids covering 207,107 km^2 of forested area. The field data were then spatially attached to the grids in a GIS platform (ArcGIS ver. 10.6.1).

We procured spatial presence information of Lantana from its native and global invaded range from the Global Biodiversity Information Facility Portal (accessed through GBIF.org (May 11, 2018) GBIF Occurrence Download https://doi.org/10.15468/dl.6wjkzt). Occurrence data with accurate geolocation obtained after the year 1970, within a comparable temporal range of the climate data, was used for subsequent analysis. In total 11,500 occurrences were obtained for the native region, and 25,106 occurrences were obtained for invaded regions (Asia, Africa and Australia). We subsequently plotted these locations on Google Earth and selected only those locations, which were observed in forested areas of native Central America (n = 4495) and from across the global invaded range (n = 16,633) (Fig. 1). Lantana presence from ground sampling (n = 38,079) in India was added to these records to get a total of 54,712 locations of Lantana in its global invaded range. This presence information was used for developing niche models.

For modelling occupancy of Lantana, it was essential to incorporate environmental covariates that determine its occurrence in the grid. To do so, we reviewed studies that incorporate distribution modelling of Lantana in India and developed following ecological hypotheses as predictors of Lantana occurrence: a) As Lantana is native to the hot and moist areas of Central and South America, as well as since it has invaded the tropical parts of the old world, we hypothesized that its distribution would be determined by climatic factors like conducive range of temperature and precipitation. Lantana would likely prefer warm and humid areas (Goncalves et al., 2014; Kannan et al., 2013; Mungi et al., 2018; Taylor and Kumar 2013). b) As most of the warm and humid forests in India are occupied by dense woody plants, the understory shrub density is mostly determined by light availability, which is a function of forest canopy cover as well as forest degradation (Didham et al., 2005). Being an under-canopy shrub, we expected Lantana invasion to be facilitated by moderate to high light penetration through the canopy to the shrub strata. c) Studies suggest that frequent burning of forests was likely to facilitate Lantana invasion (Mungi et al., 2018). Fire in controlled conditions was also demonstrated to enable seed germination of Lantana (Hiremath and Sundaram, 2010) and could hence be an important determinant of its occupancy. d) We hypothesized that soils in which nutrient uptake was easier would be preferred by lantana (Osunkoya and Perrett, 2011). e) Human disturbances like tree cutting, tree lopping, and livestock grazing can remove the native plants thereby reducing competition and making conditions favorable for invasive Lantana (Raghubanshi and Tripathi, 2009). We use remotely sensed and global data repositories to index the above-mentioned parameters. We used minimum temperature of coldest month and rainfall of the driest quarter to represent the climatic determinants of Lantana. We indexed light availability on the below canopy strata by i) Seasonal Normalized Differential Vegetation Index (NDVI) (Huete et al., 2002) clipped by forest cover (Indian State of Forest, 2013) so as to represent canopy cover and ii) Rate of forest attrition by computing change in Gross Primary Productivity (GPP) (Heinsch et al., 2003) for the past seven years. A higher positive value of GPP change indicates improvement in forest quality while a large negative value indicates forest degradation. We obtained information on fire occurrence from the Fire Information for Resource Management System (FIRMS) database, which is a composite of daily Moderate Resolution Imaging Spectroradiometer (MODIS) hotspots and Visible Infrared Imaging Radiometer Suite (VIIRS). VIIRS detects fire at 375 m resolution using multispectral bands (Schroeder et al., 2014) and complements MODIS, which detects fires at 1 km resolution through middle-infrared and thermal infrared brightness temperature (Giglio et al., 2003). We used soil Cation Exchange Capacity (CEC) from the Global Harmonized Soil Index as an index of soil fertility (Batjes, 2009). We used tree cutting, tree lopping and livestock grazing information recorded during the field sampling to incorporate the role of disturbance in facilitating the invasion by Lantana. All covariates were resampled to 25 km^2, the scale of inference used throughout in this paper. Subsequently, we estimated the correlation amongst different covariates, and used only those covariates for which the Pearson's Correlation Coefficient (r) was insignificant ($-0.7 > r > 0.7$). In case of correlated covariates, only one was used. Details on the source, scale and relevance of these covariates are provided in Supplementary material 1, Table S1.

2.2. Occupancy modelling

The number of sampled plots within 25 km^2 grids ranged between 1 and 31. Since these plots were small as compared to the grid size, there was a possibility of sample plots not detecting Lantana presence in a grid, when in fact it was present outside the sampling plots in a grid (MacKenzie et al., 2017). We explicitly account for detection bias by modelling and correcting for detection probability of Lantana. We modeled Lantana occurrence with covariates as a logit link function in the program Presence (Hines and MacKenzie, 2006). In order to reduce the redundancy of information and model complexity, only one covariate of a significantly correlated pair ($-0.7 > r > 0.7$) was used in the model. Covariates representing each of the major factors (climate, soil, forest attributes, and human disturbance) were used by themselves, and together to construct ecologically meaningful models. Covariates that substantially and parsimoniously improved model fit to the observed data based on Akaike information criterion (AIC) (Akaike, 1973) were retained. Model with least AIC was considered to be the best model (Johnson and Omland, 2004) that explained occurrence of Lantana. When models differed by < 5 AIC, we used model average estimates weighted by AIC weights to incorporate model uncertainty in parameter estimates (MacKenzie et al., 2017). We used bootstrap function to generate 1300000 iterations for evaluating the goodness of fit of the best model to our data and used $\hat{c}$ statistics to correct for over dispersion, if any (MacKenzie et al., 2017).

2.3. Species distribution modelling

To get an estimate of areas suitable for Lantana that were not sampled by ground surveys; as well as for comparing niche disparity and similarity between the native and invaded ranges, we used Maximum Entropy (MaxEnt) (Elith et al., 2011; Phillips et al., 2004), one of the most widely used algorithms for niche modelling. MaxEnt calibrates environmental variables from species presence locations and compares them with a set of random sample locations from the study area (Presence-background model). It uses this calibrated relationship of species presence with environment variables to seek similar locations that would likely support the target species. The most unconstrained model developed is considered as the MaxEnt model (Phillips and Dudík, 2008).

We divided the Lantana presence into three subsets based on the regions considered: native region (the central American), Indian invaded region (the tropical India) and global invaded range (Africa, Asia and Australia). Being presence-background model, the range of background environment substantially influences the response curve and subsequent distribution modeled through MaxEnt. It necessitates appropriate ecological criteria and sampling strategy to define the background (Elith et al., 2010; Webber et al., 2011). Since we only consider forested landscapes for this manuscript, background points were obtained only from the forested areas of the regions considered. Since, Lantana was not sampled systematically across its global range and to avoid any bias in our model by having background points that may come from areas underrepresented in our sampling, we first modeled the kernel density of our sampling locations and specified the model to select background points from within this kernel surface in proportion to our sample distribution after dropping the pixels in which Lantana was detected. Within each region, we modeled the kernel density of the presence locations using kriging and used this surface to select background points. By doing this, we eliminate the effect of outlier in the environmental covariates that can result in overfitting the distribution of species. Within forests defined by this surface, we randomly selected 10,000 points (no more than one in 1 km^2) to estimate the background environment in each region. The covariates from these background data were used to define the available environment for modelling climatic and ecological niches. Lantana presence points determined the selection of niche space in this environment by the species.

In order to avoid autocorrelation of the GBIF records, which tends to be biased towards more visited popular areas, we randomly selected only one presence within each pixel area (1 km^2) in all regions. We randomly divided the presence locations into training (80%) and testing (20%) sets, using k-fold partitioning design, with $k = 5$. We used each k-partitioned presence as an input data for MaxEnt. In the present study, linear and quadratic features were used to generate the MaxEnt model with 100 replicates for each model. Different thresholds of regularization parameter result in different MaxEnt output, where with increase in the regularization parameter, the output probability distribution gets smoothened (Elith at al. 2010). We built multiple models using these presence locations and covariate information with regularization parameter set as 0.25, 0.5, 0.75, 1, 1.25, 1.50, 1.75 and 2. MaxEnt modeled niche suitability as a probability for every pixel that varies from 0 to 1. In the present study, all pixels of the output raster that were greater than a threshold provided by the 10th percentile training presence, were considered as potential suitable regions. Though somewhat subjective, these threshold criteria were considered as a robust cutoff in previous studies on Lantana in parts of India (Panda et al., 2018; Mungi et al., 2018). We further estimated the True Skill Statistics (TSS) for every model output in the Indian and global invaded region, wherein we used the confirmed occurrence location of Lantana from the ground surveys/GBIF and assessed the proportion of accurately classifying the testing data (20% data) (Liu et al., 2013). Area Under the Curve (AUC) of the MaxEnt model was considered as an additional criterion to assess the ability of the MaxEnt model to predict Lantana presence for each region (Hosmer and Lemeshow, 1989). For Indian and global invaded region, we used the TSS as a primary indicator of accuracy and AUC as secondary, and rank different MaxEnt models generated with different settings of the regularization parameters, to select the model that yielded best TSS and maximum AUC. This regularization parameter was then used to model Lantana distribution in native region as well.

2.3.1. Regional ecological niche

We define the species' realized ecological niche as the space, where the species is constrained by abiotic and biotic factors (Colwell and Rangel, 2009). We used the native and Indian invaded region to estimate the difference in realized niche, as we intend to understand the change in species relationship with its overall available environmental predictors using its realized niche. First, we used the presence points in the native range ($n = 2572$) along with climatic covariates (annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest quarter and precipitation of driest quarter), soil CEC, summer NDVI, fire frequency and cumulative loss in GPP, in the above described MaxEnt settings. This provided us the realized ecological niche of Lantana in its native region. In order to understand the areas available for Lantana in India, we projected this native ecological niche of Lantana to all forested areas of India. We call this the potential ecological niche of Lantana in India. Secondly, we used the surveyed Lantana presence ($n = 7238$) with the same environmental covariates (used for the native range model) in India to model the observed ecological niche of Lantana. Realized ecological niche represents suitability of area for being invaded by Lantana. We used it as an index of Lantana invasion in non-surveyed forests of India, as it was derived from a training sample of Lantana presence in surveyed forests and its eco-climatic covariates.

Further, we compared the relation between Lantana occurrence probability and environment covariates in its native and invaded range, also often known as functional response traits (Keddy, 1992; Lavorel and Garnier, 2002). For this, we used the response of Lantana to maximum temperature of warmest month as an index of thermal tolerance; soil CEC as an index of nutrient transfer; and pre-monsoon NDVI as an index of tolerance to the dense canopies (as explained earlier for occupancy models). In addition to this comparison of response, we plotted the distribution of Lantana along these variables in its native and invaded range and compared the difference in the distribution using a Student's t-test in the R ver. 3.5.0 environment (R Core Team, 2018).

2.3.2. Global climatic niche

We define a species' climatic niche as the set of climates in which the species currently exist in its native range (Atwater et al., 2018). Unlike the covariates of ecological niche, to which the species can likely adapt in a shorter span of time and differentially in different ecological settings, adaptation to climatic covariates are known to take longer time and have an evolutionary footprint on the species (Gallagher et al., 2010; Mandle et al., 2010). However, the evidences of change in the climatic niche are shadowed by the statistical limitations arising from data bias due to comparisons in climatically non-analogous areas.

To establish a valid comparison between the native and global invaded range, we defined the analogous climatic area by considering the following variables: annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest quarter and precipitation of driest quarter for native and global invaded region (40^0 N to 60^0 S) at 30 Arc-second resolution (~1 km^2).

For every pixel from within the native and global invaded region of Lantana, we extracted the values of the above-mentioned variable as well as information on the occurrence of Lantana in that pixel. The entire set of these pixels from native and invaded range was then collated for each of the climatic variable. Principal components (PCs) were then extracted from the combined dataset of native and invaded range for all climatic variables to reduce dimensionality and redundancy of information (Jolliffe, 2002). PCs that had Eigen values > 1 were further used for assessing climatically analogous areas in native and invasive range. Subsequently, pixels with Lantana from the native and invaded range were plotted on the PC axes to visually discriminate them on the climatic niche axes. A formal analysis to identify analogous climatic space was undertaken using four different methods; NicheA, Mobility-Oriented Parity (MOP), Multivariate Environmental Similarity Space (MESS) and ExDent tool. NicheA generates two convex polyhedrons around the native and invaded climatic space, and estimates the overlap between polyhedrons, which represents similar climatic conditions in both the ranges. This overlapping climatic area of the polyhedrons was projected to the geographic space of both the native and global invaded region to identify analogous areas (Escobar et al., 2016). MOP measures Euclidean distances between climatic space of native and invaded range and excludes that climatic space, which is outside the calibration region (Owens et al., 2013). MESS identifies dissimilar areas based on the statistical distance of climatic variables in native and invaded range from their common mean value (Elith et al., 2010). While these three methods identify univariate similarity in two areas, there might be a novel climatic combination not present in the native region, but only in the global invaded region; and is not addressed by using the abovementioned three methods. ExDent tool addressed this correlational similarity and helped identify climatic combinations that are novel in the global invaded region, as compared to the native region (Mesgaran et al., 2014). We subsequently visualize the output of these four methods for the Indian invaded region to understand the parity between the similar areas identified. The final area identified as analogous between the native and global invaded region was derived by intersecting the results obtained by these four models, in ArcGIS 10.6.1. This final analogous area was used as a conservative model of similar climatic surfaces for modelling and comparing climatic niche of Lantana.

We used the analogous areas between the native range of Lantana and its global invaded range to compare its potential climatic niche with the observed climatic niche. For this analysis we used presence locations of Lantana from its native range ($n = 2572$) and the climatic variables (annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest quarter and precipitation of driest quarter) in MaxEnt, and projected this native climatic niche across the global invaded region. Subsequently, we used Lantana presence ($n = 17{,}895$) from across its global invaded region to model its observed climatic niche using the same climatic covariates used for modelling in its native range. The difference in potential and observed climatic niche of Lantana across its global invaded range was estimated by using Schoener's D and Hellinger's distance I metrics available in 'phyloclim' package of R 3.5.0 (Heibl et al., 2013, R Core Team, 2018). Secondly, the percentage of Lantana presence points that were not classified as presence by native climatic niche were used as an estimate of niche expansion within the analogous niche space in the invaded range.

We used analogous climatic space between native and invaded areas to compare and understand Lantana's response to bioclimatic variables. However, we also modeled climatically suitable areas for Lantana outside of this analogous space based on its global occurrence data. For this we used global occurrence ($n = 30{,}116$), bias sampling mask file for MaxEnt to select background points (Elith et al., 2010), and the best regularization parameter determined by MaxEnt, using the aforementioned method. This approach allowed us to estimate the global potential area that could be invaded by Lantana.

3. Result

3.1. Occupancy modelling

Out of 13,715 grids surveyed, Lantana was detected in 5334 grids (Fig. 2a) giving a naïve occupancy estimate of 38.8%. Of the total 207,100 km^2 forest surveyed, Lantana was detected in 86,806 km^2. The model that best explained Lantana presence while correcting for imperfect detections differed from the next competing model by ΔAIC of 207, and from the null model by a ΔAIC value of 810 (Table 1). Lantana occupancy was best explained by a) Climatic variables: higher rainfall in the driest quarter and warm winters; b) Soil fertility surrogated by CEC and c) human impacts surrogated by lopping and decline in GPP (Table 2). The model inferred Lantana occupancy was estimated to be $\psi = 39.39\%$ (SE 0.2). With high detection probability (64.3%), the increment in Lantana occupancy from 38.8% naove estimate to 39.39% model inferred estimate was little. Since the survey was limited to forested areas, this occupancy estimate depicts Lantana presence in forests of 18 Indian states. The bootstrap distribution of 1300000 runs from the best model did not differ from the observed data, suggesting that the model was a good fit (goodness-of-fit test, $P = 0.13$) and the $\hat{C}$ statistic was 0.97, suggesting absence of over-dispersion. Out of the total 207,100 km^2 of surveyed forest, 86,831 km^2 forests had high occupancy probability of Lantana with $\psi > 0.5$; 68,006 km^2 had low occupancy probability with $0.1 < \psi < 0.5$ and in 52,270 km^2 Lantana was practically absent, where $\psi < 0.1$. (Fig. 2b).

3.2. Regional ecological niche

Highest modelling accuracy, as depicted by $TSS = 0.69$ (± 0.04), was when the regularization parameter was kept at 1. Minimum temperature of coldest month, soil CEC, maximum temperature of warmest month, pre-monsoon NDVI and loss in GPP explained more than 80% of Lantana presence in its native and invaded Indian range (Suppl. material 1, Table S2). Lantana's ecological niche model trained on its native environment had an $AUC = 0.80$ (± 0.06), suggesting a good model fit. When projected to India, this potential ecological niche was a subset of its realized ecological niche, which in turn had a good model fit ($AUC = 0.73 \pm 0.01$, $TSS = 0.68$). Furthermore, the realized ecological niche in India estimated the area suitable for its invasion outside the surveyed area to be 148,770 km^2 (Fig. 2c).

The relationship of Lantana occurrence with covariates differed substantially in magnitude and form between its native and invaded range (Fig. 3). In case of temperature of warmest month, the distribution in India significantly exceeded (P-value < 0.005; Fig. 3c) the upper range of distribution in Central America (41 °C; Fig. 3a and b). Lantana showed a parabolic relationship with soil CEC in its native range (Fig. 3d) with maxima at 50 $meq^+/100$ g, while in India the relationship was a reverse parabolic with CEC (Fig. 3e); however, the difference in distribution against soil CEC was insignificant (P-value > 0.9; Fig. 3f). In case of pre-monsoon Normalized Differential Vegetation Index (NDVI) that represents canopy cover, the distribution of Lantana in India was seen to be constrained within a small range which is significantly different subset ($P = 0.1$) of its distributional range in Central America (Fig. 3i). However, within this range, the response of Lantana to NDVI has changed. Lantana distribution in Central America increased with NDVI till the threshold of 0.2, after which it decreased (Fig. 3g); while

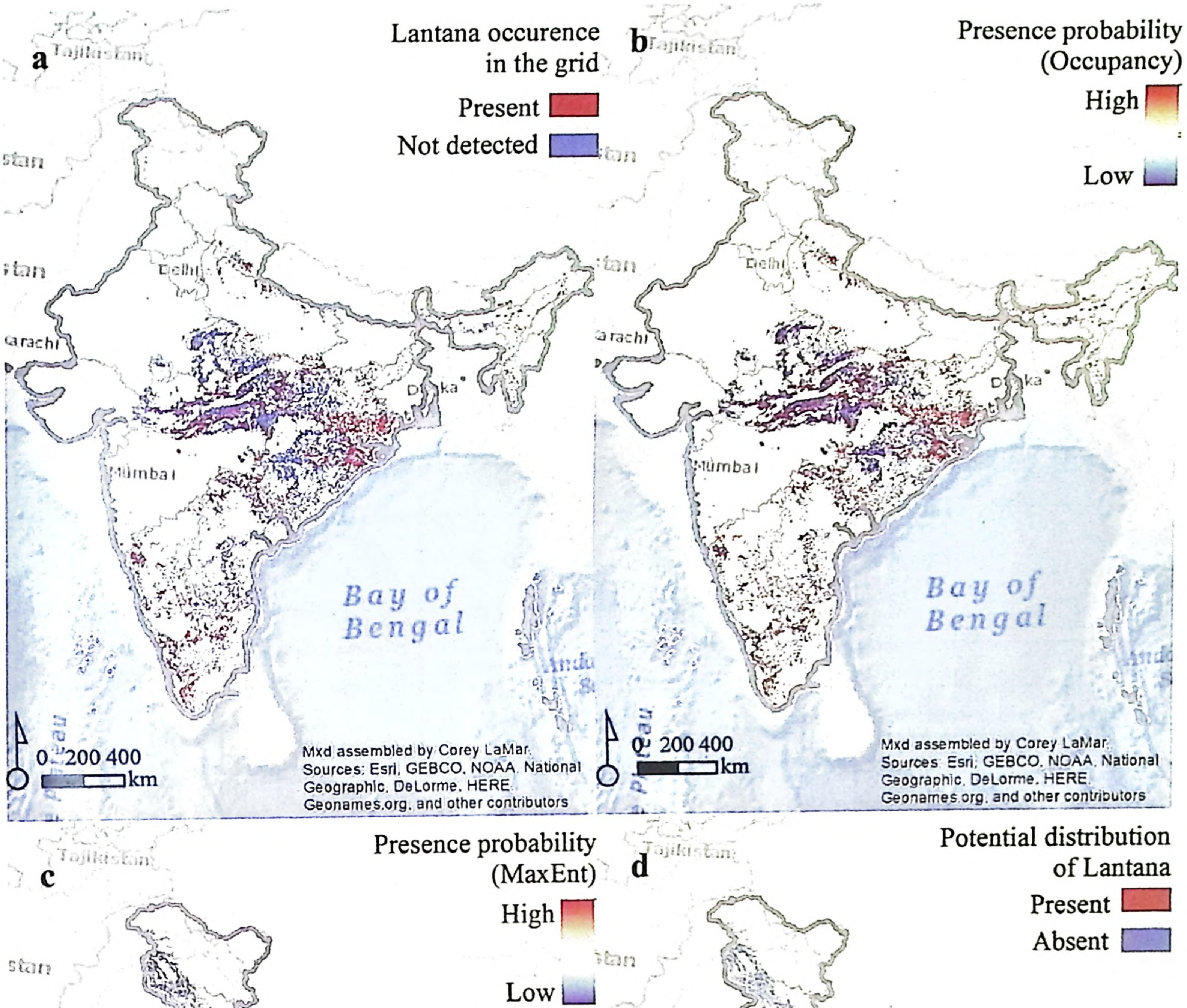

Fig. 2. *Lantana camara* distribution in India. (a) Grid cells with Lantana presence (red) and where Lantana was not detected (blue), (b) Potential distribution of Lantana corrected for imperfect detection and site covariates in an occupancy framework (c) Areas susceptible for Lantana invasion modeled by MaxEnt for non-surveyed area using the information from surveyed area and, (d) An aggregated distribution of Lantana in forests of India, obtained by ensembling occupancy estimates for ground surveyed areas (in the year 2010) and MaxEnt models beyond ground surveyed areas.

Table 1
Model selection statistics of various models used to *Lantana camara* occupancy in tropical India.

Model covariates	AICestimate	Δ AIC	No. Par	−2 X loglikelihood
Null model				
ψ (.) P(.) Null model	79414.2	810.1	2	79410.2
Climate				
ψ (Precipitation of driest quarter (PD)). P(.)	79102.5	498.5	3	79096.5
ψ (Minimum temperature of coldest month (TM)). P(.)	79139.3	535.2	3	79133.3
ψ (PD + TM). P(.)	78836.2	232.2	4	78828.2
Soil				
ψ (Soil fertility (CEC)). P(.)	79374.2	770.2	3	79368.2
Anthropogenic Disturbance				
ψ (Tree lopping (TL)). P(.)	79401.5	797.5	3	79395.5
ψ (Tree cutting (TC)). P(.)	79428.9	824.8	3	79422.9
ψ (Livestock seen (LS)). P(.)	79284.4	680.4	3	79278.4
ψ (Number of human trails (HT)). P(.)	79377.2	773.1	3	792371
ψ (Cumulative loss in productivity (GPP)). P(.)	79076.5	472.5	3	79070.5
Combined climate, soil and anthropogenic disturbance				
ψ (TL + TC + LS + HT + PS). P(.)	79203.4	599.4	7	79189.4
ψ (PD + TM + CEC + TL + TC + LS + HT + PS + GPP). P(.)	78811.5	207.5	11	78789.5
ψ (PD + TM + CEC + TL + GPP). P(.)	78604.1	0	7	78590.1

Table 2
Coefficients of the best model that explained *Lantana camara* occupancy, while accounting for imperfect detections. Coefficients are listed in reducing order of importance following the intercept.

Covariates	Coefficient estimate	Standard error
Constant (Intercept)	−0.444	±0.018
Rainfall of the driest quarter	0.316	±0.02
Minimum temperature of coldest month	0.26	±0.019
Soil cation exchange capacity	0.036	±0.019
Average lopping	0.016	±0.018
Cumulative loss in productivity	−0.287	±0.02
Detection Coefficient	0.587	±0.01

in India the threshold was observed to have shifted to 0.7 and the response was a linear increase with a short asymptote (Fig. 3h).

3.3. Analogous areas in native and invasive range

Three Principal Components cumulatively explained 99% of the variance in the climatic data in native and global invaded region (Suppl. material 1, Table S3). The first PC comprised areas with increasing annual precipitation and decreasing temperature; the second PC represented wet areas that have lower annual temperature and winter temperature; and the third PC represents areas with increasing annual precipitation and reducing aridity (higher rainfall in driest month) (Fig. 4). These PCs were used for assessing the climatically analogous areas in native and invasive range. When the subset of results for India was explicitly visualized for the four models (NicheA, MOP, MESS and ExDent) to see consistency in identifying areas of similar climatic conditions, the models were consistent in identifying a common analogous climate area in the drier areas in western and southern India, the Gangetic river basin, northeastern hills and the Eastern Ghats (Suppl. material 1, Fig. S1). In doing so, the largest dissimilar area was identified by ExDent, followed by MESS, NicheA and MOP. An intersection of these model helped derive the largest dissimilar climatic surface, and remove from the analysis of niche comparison.

3.4. Global climatic niche

Highest modelling accuracy, as depicted by TSS = 0.72 (±0.05), was when the regularization parameter was kept at 1. Annual precipitation and precipitation of the driest month together explained more than 90% of the global Lantana distribution (Table S4). The climatic niche model of Lantana had an AUC = 0.74 (±0.01) in native region, and an AUC = 0.70 (±0.02) and TSS = 0.76 in global invaded region. The native niche when projected on the global invaded region (Fig. 5a) was found to be a subset of the observed global invaded climatic niche of Lantana (Fig. 5b). Within the invaded range 58% (±6%) Lantana presence points were outside the projected native climatic niche of Lantana. The Hellinger distance I and Schoener's D value of similarity in potential and observed climatic niche of Lantana was 0.39 and 0.42 (P-value = 0.12), suggesting an ecologically relevant, but statistically insignificant difference.

For the global model, highest accuracy as depicted by TSS = 0.66 (±0.08), was when the regularization parameter was kept at 1. Annual precipitation, precipitation of the driest quarter and temperature of the coldest month together explained more

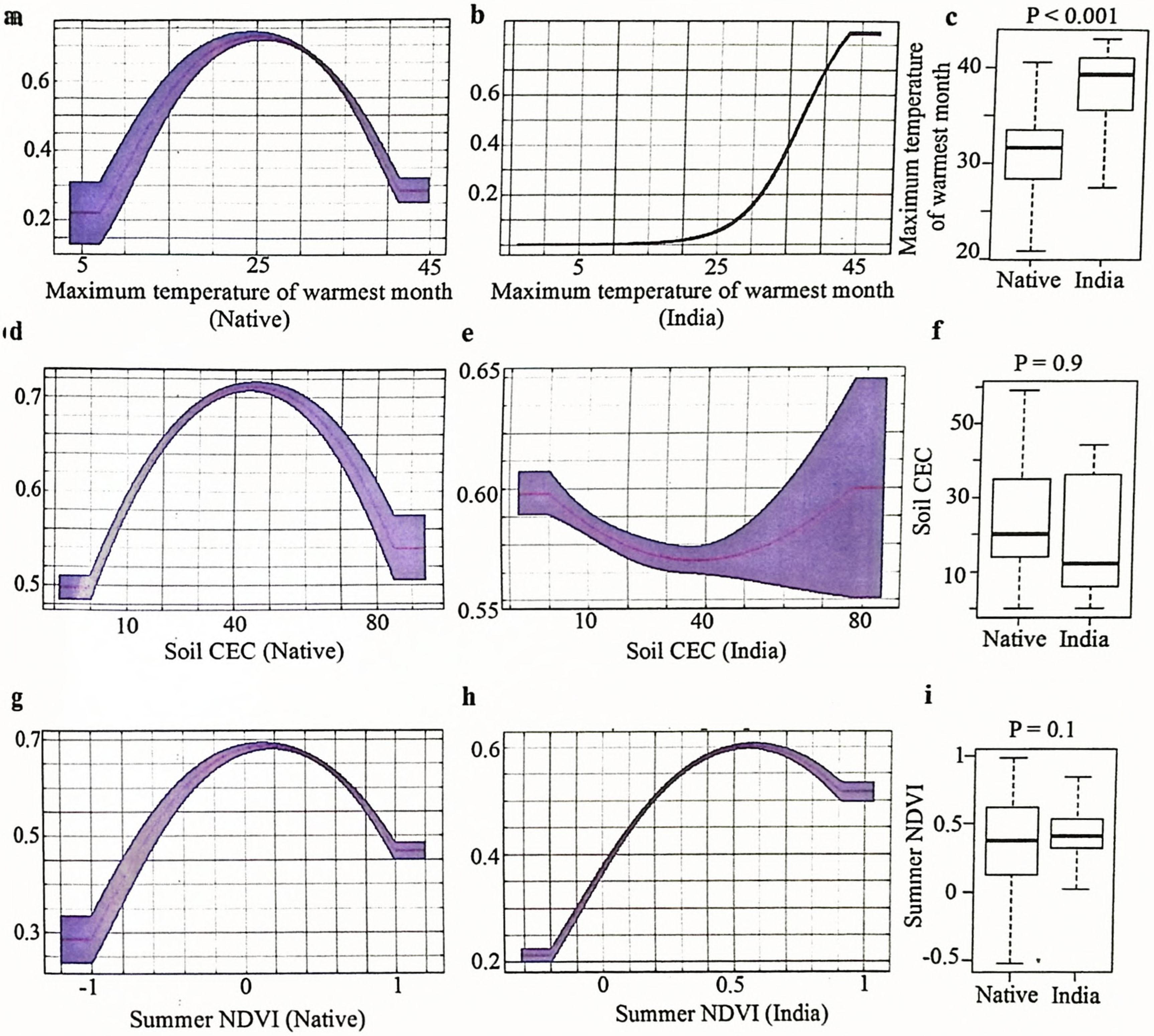

Fig. 3. Response of *Lantana camara* heat tolerance, soil fertility, and light availability in native Central America and in invaded India. Response of Lantana to highest temperature in the warmest month in Native America (a), Invaded India (b), and the box plot showing the increase in high temperature tolerance in India (c); Response of Lantana to soil Cation Exchange Capacity (CEC) in native America (d), observed in India (e), and the box plot showing Lantana distributed within the same range in Native America and invaded India (f); With regard to summer Normalized Differential Vegetation Index (NDVI) Lantana decreased with increased NDVI in native America (g) and increased in invaded India (h), but the niche width of Lantana with respect to NDVI was similar (i).

than 90% of the global Lantana distribution (Table S5, response curves provided in Fig. S2). This climatic niche model of Lantana had AUC = 0.62 (±0.02). Across the global range, an area of ~11,631,000 km^2 (10,898,000 to 12,225,000 km^2) was found to be climatically suitable for Lantana invasion (Fig. 5c, Fig. S3). Within countries, highest suitable areas available for Lantana were in: India (~1,351,000 (1,303,000 to 1,381,000) km^2), Australia (~867,980 (790,000 to 929,000) km^2), China (~317,970 (283,770 to 349,790) km^2), Mozambique (~287,280 (263,170 to 311,250) km^2), Madagascar (~244,360 (223,670 to 261,710) km^2), Ethiopia (~241,070 (212,230 to 265,390) km^2), Myanmar (~183,750 (165,550 to 195,330) km^2), Vietnam (~106,340 (98,130 to 111,260) km^2), Tanzania (~104,850 (87,560 to 121,490) km^2) and South Africa (~98,710 (88,080 to 107,100) km^2).

4. Discussion

Lantana invaded 86,806 km^2 forests (38.8%) of India, particularly degraded forests of hot and humid areas. It was widely distributed across landscapes with maximum invasion in fragmented dry deciduous forests of Central India, Shivalik hills and

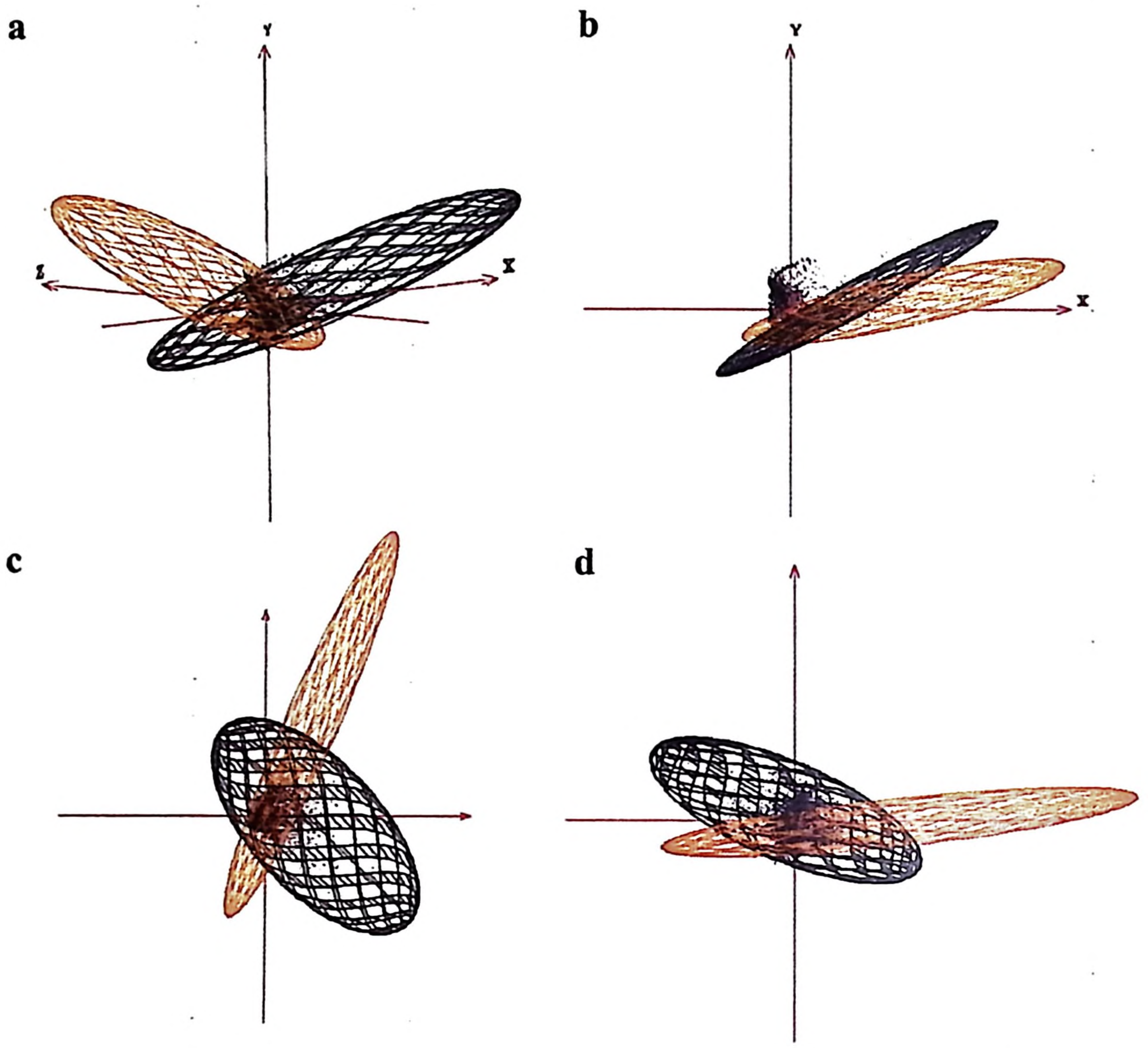

Fig. 4. Distribution of *Lantana camara* along the three principal components representing climatic factors of native (Central America: yellow polyhedron) and global invaded region (Africa, Asia and Australia: black polyhedron). Grey points represent climatic space not occupied by *Lantana*. Axis X represents increasing annual rainfall and increasing temperature, axis Y represents increasing cooler winters and axis Z represents reducing aridity (Suppl. material 1, Table S3). Visualization of distribution on (a) three-dimensional climatic axes, (b) X and Y axis, (c) Y and Z axis, and (d) X and Z axis.

Southern Western Ghats. Relatively lesser area was recorded to be invaded in the Northeastern tropical forests, Northern Western Ghats, semi-arid and arid landscapes of Western India (Fig. 6). With this large invaded range, Lantana is probably the most widely distributed invasive plant in India, as compared to other invasive plants (Mungi et al. 2019; Mathur et al., 2015). Addition of the recorded locations of Lantana from India to the global presence locations, revealed that an area much larger than ever recorded was suitable for Lantana invasion. This expansion in its invaded range was found to be correlated with its increased tolerance to higher temperatures, lower fertility and denser canopy cover as compared to its native range. For an invasive species, change in its thermal tolerance and resource preference within a short span of time poses an interesting question on its plasticity and/or adaptability, which in either case suggests that a larger area could be globally invaded with time. Our results highlight the role of forest degradation and climate change in elevating the global risk of biological invasions, and the importance of large-scale ecological monitoring for a better understanding of invasions that can potentially guide management actions.

In the case of Lantana, we sampled plots of 10 m diameter ranging between 1 and 31 within each 25 km^2 grid cell. Detection within each of these plots was not a concern as Lantana presence would be detected without bias, but it was possible that the placement of plots missed Lantana occurrence within the 25 km^2 grid. Occupancy analysis explicitly addresses the limitation of imperfect detection, while providing insights into relationships of occurrence with covariates (MacKenzie et al., 2017). We found that the average detection probability by a single plot for a grid was 0.64 (SE 0.03) and bias resulting from imperfect detection was negligible as the model inferred occupancy estimate of Lantana differed from the naive estimate by only 0.71%. Thus, we probably missed detecting Lantana on 92 out of 13,715 sampled grids. The total forested area in the 18 states covered 15,312 grids, out of which 13,715 were sampled, which amounted to ~81% of total forested area being sampled. The unsampled grids were either under political unrest or inaccessible due to logistic constraints. The occupancy model helped us understand the potential status of Lantana in these areas. The occupancy covariates enhanced our understanding on factors that facilitated and limited the occurrence of Lantana in India at a scale of 25 km^2, which is relevant for ecological understanding and management interventions. MaxEnt models rely on presence information, modeled against the background with covariates to predict suitable sites where the species can potentially occur (Elith et al.,

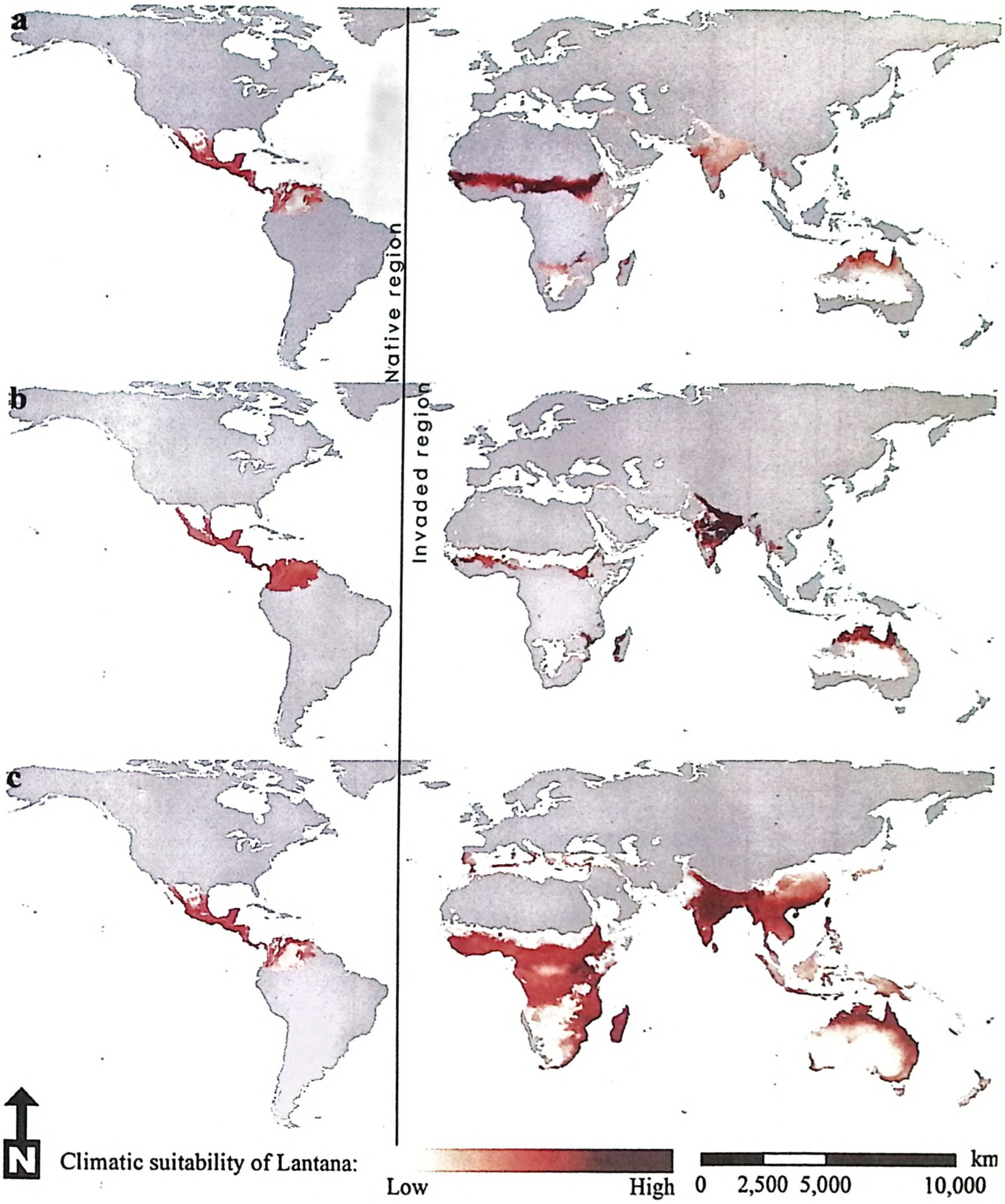

Fig. 5. Climatic niche of *Lantana camara* in its global range: (a) climatic niche of Lantana modeled from presence in the its native range and projected to analogous areas in its global invaded range (b) climatic niche of Lantana in analogous areas of its global invaded range as modeled from its presence in these areas (c) global climatic suitability of Lantana modeled from its global presence).

2011). Additionally, occupancy models also consider imperfect detections and therefore, are more reliable. For this reason, we used occupancy-inferred presence within 207,100 km^2 of forests that were ground surveyed and MaxEnt inferred suitable areas for invasion within the remaining 494,573 km^2 to get the most reliable total estimate of areas threatened by Lantana invasion to be 303,607 km^2 in forested landscapes of India (Fig. 2d).

Previous studies used climatic niche model of Lantana as a surrogate for its distribution (not as potential habitats) using a limited number of secondary or primary occurrence data (e.g. 2526 locations by Panda et al. 2018; 2526 locations by Bahuguna, 2015). These studies suffer from paucity of data and faulty inferences from the models. In the current study, we used data that were obtained from one of the largest known systematic sampling for any invasive plant. Thus, the ground

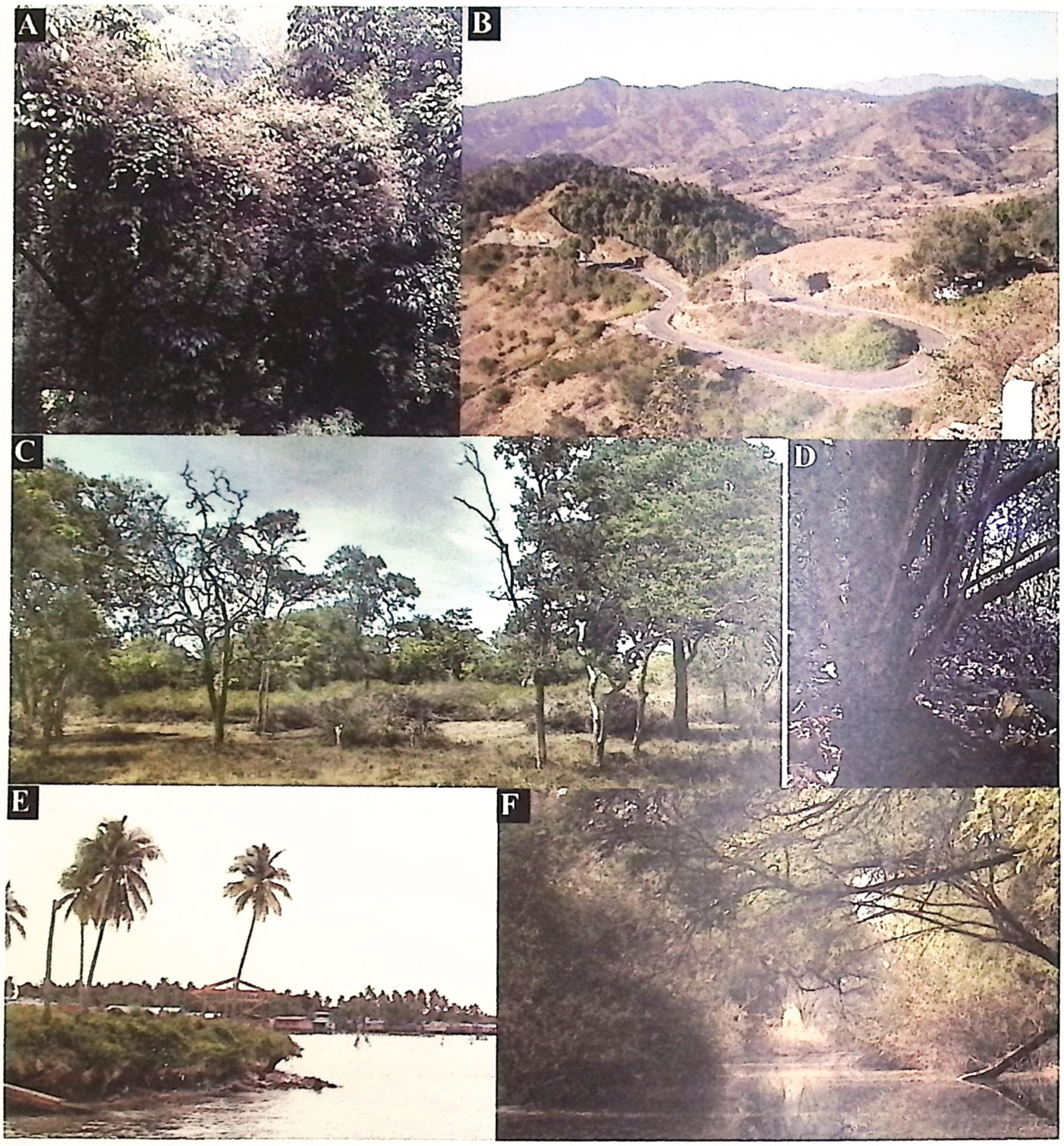

Fig. 6. Diverse habits and habitats of *Lantana camara* in India: Lantana was recorded in different habits across different biogeographic realms in India. Here we show the climber ecotype of Lantana in evergreen forests of the Western Ghats (A); shrub ecotype in the Western Himalaya (B) and dry savannas of Central India (C); Tree (bole girth > 15 cm) ecotype in the mesic savannas of central Indian highlands (D); short shrub ecotype on the coastal sand dunes (E); and emergent shrub ecotype in the wetlands of semi-arid India (F).

validation data we used is much larger and from across an ecological scale relevant for modelling multi-landscape distribution. We subsequently used a robust approach to model-based inference using ecologically relevant covariates (e.g. Qiao et al., 2017; Beck et al., 2014).

Furthermore, previous few studies have attempted modelling the global distribution of Lantana using proportionally fewer occurrences from India from a smaller geographical extent, and this is likely the scenario of data from other countries as well (e.g. Taylor and Kumar 2012; Taylor et al., 2012; Bhagwat et al., 2012; Taylor and Kumar 2014, Goncalves et al. 2014, Qin et al., 2016). By the use of a substantially larger training dataset the reliability of our inferences are better than previous estimates and with the associated uncertainty. The climatic niche of Lantana in its global invasion range was substantially larger than the one projected from its native region. This expansion was estimated only in the climatically analogous areas of its native and invasive range, thus having a statistical power to highlight the expansion. As compared to previous global projections, we show that Lantana could potentially invade novel climatic regions in India, Myanmar, Thailand, Philippines, Pakistan, Northern Australia, Madagascar, Mozambique, Malawi, Ethiopia and parts of Oceania. Our global potential niche revealed large extent in Nigeria, Mali, Gambia, Sudan, and surrounding countries, from which Lantana presence was not available. This could either be due to paucity of sampling in these areas or actual absence. Future invasions in these countries should be monitored in order to arrest the invasion in its initial phase. It is also possible that Lantana has already invaded many of these potential areas which have not yet been sampled for occurrence. Our models highlight such areas across the world which should be sampled on priority. Across its invasive range, the expansion was partial towards warm and humid climatic areas and coincided with mesic savannahs in the region.

As a consequence of the ongoing global climatic changes, the countries invaded by Lantana are prone to warmer winters and rainfall in the driest season (Devraju et al., 2015), which in turn will elevate the humidity of an area (Jin and Wang, 2018). We show both of these traits to facilitate the invasion of Lantana across its global range. Management of Lantana, in India costs ~$18,700 per km^2 (Babu et al., 2009). With the current expanse, the cost estimate of Lantana management exceeds $5.5 billion in India (which exceeds the annual fund allocation to the Ministry of Environment, Forest and Climate Change, Government of India, for the year 2019 by a factor of 10 India), and proportionately more globally. While management of Lantana can be a costly affair, its invasion in novel climatic areas elevate the financial investment as more and more areas could be invaded by it. It further raises an ecological conundrum of managing a species that is potentially evolving to the regional environment (Mungi and Qureshi, 2018). Many scholars suggest that if a species is evolving to the ecological settings of the landscape, and is being used by other species, one can categorize it as a novel 'native species' evolving in the times of global changes (e.g. Pearce, 2016). These arguments might prevent any control mechanisms to arrest the invasion and can potentially lead to decline in the native biodiversity. Hence, it is critical to understand the reasons for Lantana's potential adaptability and invasion success.

The observed success of invasion, like in many other cases, can be interpreted in the light of availability of suitable niche, inherent phenotypic plasticity that optimizes the fitness in the new environment, and/or contemporary adaptation to new conditions (Hulme and Barrett, 2013). In India, most of the forests are used by local communities for livelihood and many areas are degraded by ecologically unsustainable uses of varying degrees (DeFries et al., 2010; Agarwala et al., 2016). In such areas the threat of Lantana invasion is higher, as inferred from our occupancy and MaxEnt models. Besides Lantana occupancy being promoted by human disturbance-induced degradation of native forests, it was also enhanced by warmer and more humid climates. Thus, the success of Lantana invasion in India is likely attributed to increasing availability of suitable climate and facilitation by reduced competition through human induced degradation. Unlike other tropical developing countries, where forested areas are reducing due to increased developmental activities, forest area in India was reported to increase at a rate of 1120 km^2/year over the last decade (FSI, 2019). We flag the increase shown in the forest cover, which differentiates between plantations and invasive plants should be a vital element for long-term monitoring. Currently, we believe that these distinction between native forest, forest plantations and forest dominated by invasive species are not differentiated appropriately to justify increase in forest cover. We show that forest degradation caused by anthropogenic activities and/or global climatic changes could be in fact converting the native forests into invaded green patches, which could be mistaken as forest (e.g., Koulgi et al., 2019). This confusion can mislead forest policy, investment in management actions and subsequently compromise conservation objectives.

The climatic niche is used as a proxy for the fundamental niche, which is bounded by the environmental tolerances of the species (Hutchinson, 1957). Hence, shifts in the realized climatic niche of species have been proposed as an indirect evidence for adaptation by invasive species to novel environments (Gallagher et al., 2010; Mandle et al., 2010). In the present case study, the climate in parts of Africa, Asia and Australia was analogous to that observed in Central America - the native range of Lantana. Within this analogous climatic space, Lantana's climatic niche has significantly expanded. The increase in climatic tolerance observed in invaded region could be due to either predator/pathogen/competition release or phenotypic plasticity or adaptive evolution. Considering the covariates representing climate, soil resources, dense canopies and disturbance by fire in India (analogous as well as novel) we found that Lantana has invaded an additional novel niche space on the axis of increasing temperature, lower soil fertility and loss of productivity of invaded forests.

Previous studies (Blossey and Notzold, 1995) suggested that escape from specialist natural enemies could result in increased competitiveness of invasive plants leading to contemporary evolution. The invaded population of Lantana was found to be more tolerant of denser canopies, which could possibly be due to its enhanced competitiveness. A phenotypic variant of Lantana in India, which is a climber, enables it to access sunlight even in dense canopied forests (Fig. 6). A recent study further demonstrated that such a phenotypic variant may increase the performance and success of Lantana invasion in forested areas (Goyal and Sharma, 2019). Moreover, as a result of global climate change, many areas are experiencing warmer summers (Sharmila et al., 2015) and increased soil acidity that results in low fertility (Bhattacharyya et al., 2015). For any invasive plant an ideal phenotypic optimum will be to exploit these changes (Corlett and Westcott, 2013; Richards et al., 2006), which was observed in the case of Lantana invasion. If the species shows a significant difference in traits between native and invaded areas it clearly indicates its phenotypic plasticity, which, if responsible for higher fitness of the species, could be considered adaptive (Sultan, 1987; Pigliucci, 2001). This adaptation could be due to inherent genetic plasticity or due to genotypic change (Sultan, 1987).

Genetic studies of Lantana in India (Ray and Quader, 2014) have found higher genetic diversity with private alleles and multiple genetic clusters across India, suggesting multiple introductions of Lantana with novel founders each time. This was further validated by naturalist records from the 19th century that indicated multiple introductions from various sources in India (Kannan et al., 2013). Another study (Ray and Ray, 2014) on Lantana in India suggested that the multiple genetic clusters could be responsible for local adaptation and it could represent early stages of ecological divergence. Thus, in addition to global climatic niche shift and shifts in response norms, both of which are suggested to be the evidence for rapid adaptation

(Pearman et al., 2008; Gallagher et al., 2010; Mandle et al., 2010), genetic evidence suggests high genetic diversity as a result of multiple introductions and probable hybridization after introduction of previously allopatric populations of Lantana. These genetic changes can also be considered as suggestive of adaptive plasticity in the introduced populations. The above evidence supports the hypothesis (De Jong, 2005) that phenotypic plasticity provides a rapid opportunity for natural selection to operate and facilitates first steps in the adaptive walk by a species, which otherwise would depend on new mutations (Travis, 1994; West-Eberhard, 2003). Nevertheless, further experiments comparing populations from native and invasive areas are required for confirming that these phenotypic changes have a genetic basis to show conclusive support of contemporary evolution.

Previous studies investigating the effects of climatic changes on invasion by Lantana assumed that Lantana-climate relation would be preserved across space and time (Kannan et al., 2013; Goncalves et al., 2014, Panda et al. 2018). Our study results flags a caution on the approach, which assumes that the niche of a species to be at equilibrium and retain its response to climate. Such assumptions could underestimate the actual threat potential of invasive species to ecosystems. Lantana has invaded around 75 countries and poses a serious threat to their native biodiversity. The methodological approach used in the current study could be adapted as a model for studying and managing Lantana and similar biological invasions elsewhere. It can lend support for encouraging national initiatives for large-scale intensive monitoring of ecosystems to inform policy and management decisions.

Declaration of competing interest

The authors declare no competing interests.

CRediT authorship contribution statement

Ninad Avinash Mungi: Writing - original draft, Data curation, Formal analysis. **Qamar Qureshi:** Conceptualization, Funding acquisition, Supervision. **Yadvendradev V. Jhala:** Conceptualization, Funding acquisition, Project administration, Methodology, Supervision, Formal analysis, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01080.

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Certificate of Participation

This certificate is awarded to Ninad Avinas Mungi............ for participation on **International Conference on Invasive Alien Species Management (ICIASM)** organized by National Trust for Nature Conservation (NTNC) from 25th to 27th March, 2014 at Biodiversity Conservation Center, Sauraha, Chitwan, Nepal.

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This is to certify that

Shri. Ninad Mungi

participated in the Workshop on

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held at State Forest Research Institute, Jabalpur, Madhya Pradesh on 13th and 14th February 2016 and successfully completed the training

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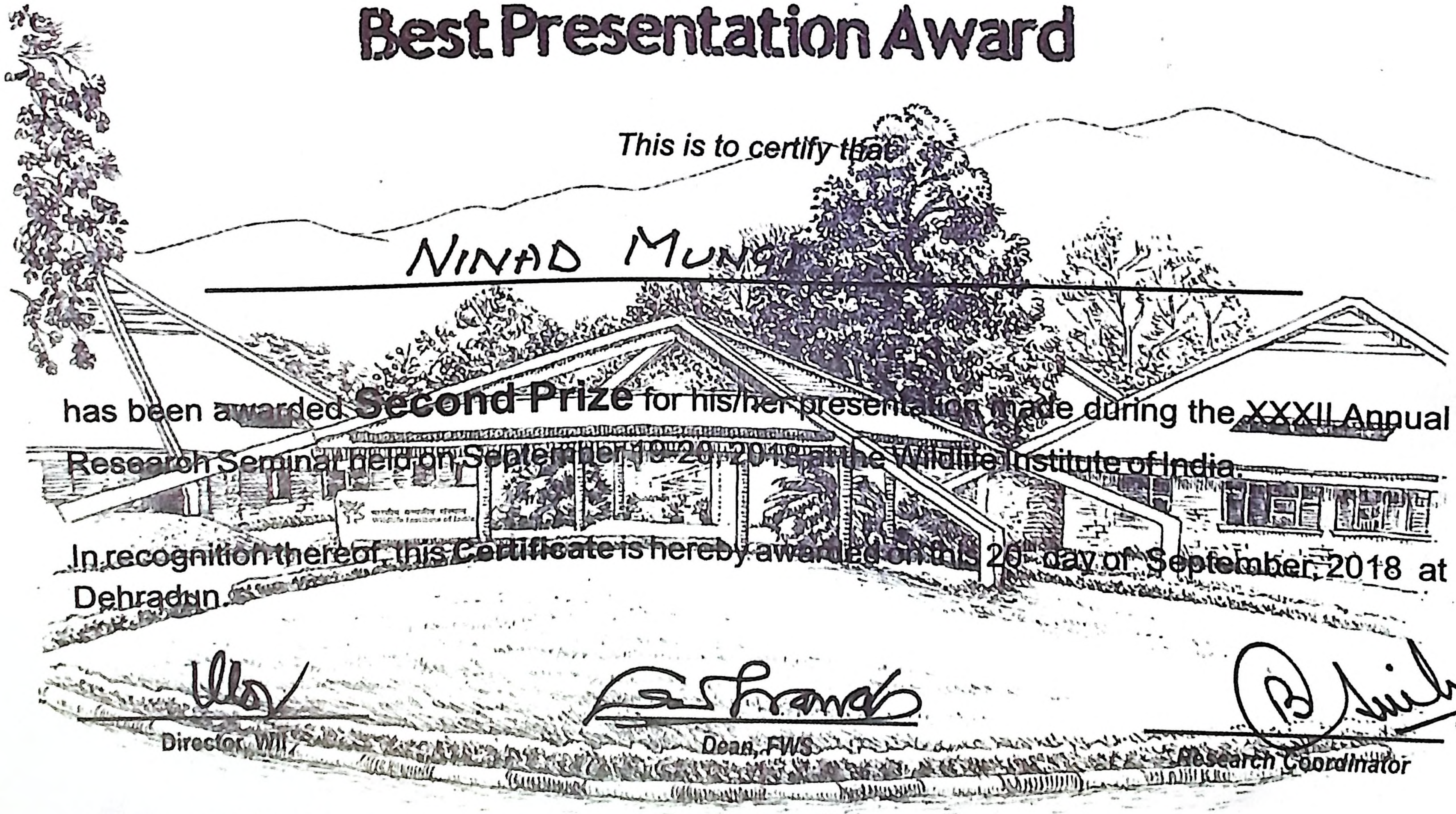
Best Presentation Award

This is to certify that

NINAD MUNG



has been awarded **Second Prize** for his/her presentation made during the XXXII Annual Research Seminar held on September 19-20, 2018 at the Wildlife Institute of India.

In recognition thereof, this **Certificate** is hereby awarded on this 20th day of September, 2018 at Dehradun.

Director, WII

Dean, FWS

Research Coordinator

American University of Central Asia

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CERTIFICATE OF PARTICIPATION

This is to acknowledge that

Ninad Mungi

participated in this conference and gave a talk titled

Tigers, Crimes and Mobile apps

Prof. Zheenbek Kulenbekov
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Abstract Title: 'All that is green, is almost invaded', shows world largest invasive plants monitoring program in India

SubmissionIdentifier: ABSTRACT SUBMISSION-3133

Dear Ninad Mungi,

Thank you for submitting an abstract for the International Congress for Conservation Biology (ICCB), to be held in Kuala Lumpur, Malaysia from 21 July to 25 July 2019.

On behalf of the ICCB Scientific Programme Committee, we would like to express our gratitude for the submission of your abstract for ICCB 2019. There were more than 1350 submitted abstracts.

We are happy to inform you that your abstract titled **"All that is green, is almost invaded', shows world largest invasive plants monitoring program in India"** was **accepted** as an **oral presentation.**

Please note that the date and time of your presentation will be sent in late-April.

Please keep this email for future reference, as it contains important information on your abstract planning.

Please note that the submitting author needs to register to the congress in order to hold the session. We kindly invite you to do so before **8 May 2019** in order to confirm your session. All speakers need to be registered in order to present. The deadline for the early registration is 17 April 2019. After this date the registration fee will increase significantly. Registration will open in late-February. Information can be found on the congress website.

For residents from some countries a visa is required for Malaysia. Please start the process to obtain a visa as soon as possible, and do not hesitate to contact us personally if you encounter any difficulty. For questions regarding visas or your registration, you may contact us at: ICCBteam@conbio.org.

If you have any questions, related to the contributed session abstract submission process or ICCB, please contact ICCBteam@conbio.org and your message will be route to the appropriate person.

On behalf of Society for Conservation Biology and the ICCB Scientific Programme Committee, we thank you again for your valuable contribution.

Society for Conservation Biology

A global community of conservation professionals

Certificate of Presentation

We confirm that **Ninad Mungi** presented an oral presentation entitled:

All that is green, is almost invaded', shows world largest invasive plants monitoring program in India

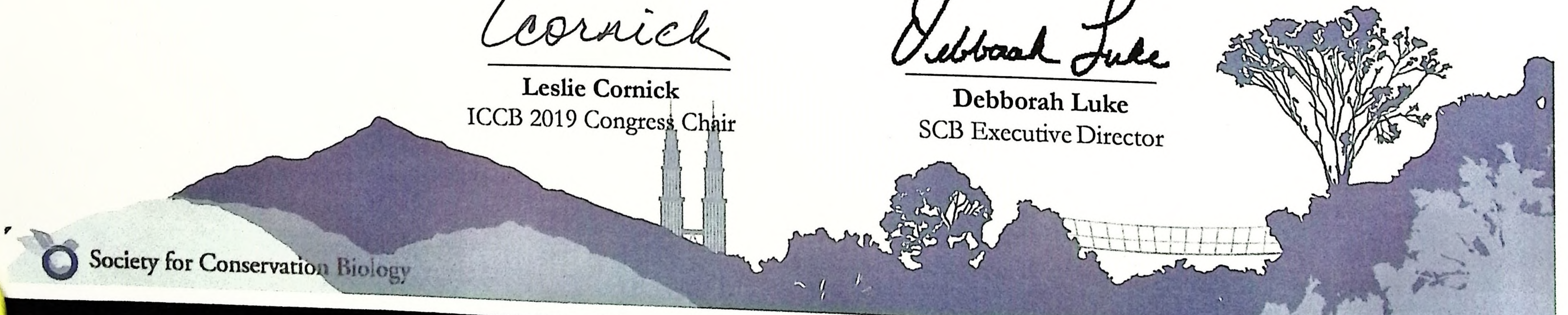
the 29th International Congress for Conservation Biology

"Conservation Beyond Boundaries: Connecting Biodiversity with Communities, Government and Stakeholders"

21-25 July 2019, Kuala Lumpur, Malaysia

Leslie Cornick
ICCB 2019 Congress Chair

Debborah Luke
SCB Executive Director



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