A Baseline Assessment of Invasive Alien Plant Species (IAPS) in Bhutan's Jigme Singye Wangchuck National Park: Distribution Patterns, Invasion Hotspots and Management Implications

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Abstract

Invasive alien plant species (IAPS) are major drivers of biodiversity loss and ecosystem degradation, particularly in biodiversity-rich and topographically complex regions. This study presents the first systematic assessment of IAPS in Jigme Singye Wangchuck National Park (JSWNP), Bhutan, based on 375 vegetation plots surveyed along 16 transects using an adaptive sampling approach. We recorded 25 unique IAPS, including four listed among the world's 100 worst invasive species. *Ageratina adenophora* was the most dominant and widespread species, present in over 60% of plots, followed by *Solanum viarum*, *Bidens pilosa*, and *Chromolaena odorata*. Species richness was highest in the southeastern and southwestern lowland zones, particularly within the Tingtibi and Nabji ranges. Chi-square tests revealed significant associations of many IAPS with altitude classes and habitat types, indicating that both environmental and anthropogenic factors influence their distribution. Spatial hotspot maps identified high-density invasion zones in disturbed and accessible areas. These findings provide a critical baseline for understanding IAPS spread in Himalayan protected landscapes and offer actionable insights for targeted management, early detection, and community-based intervention strategies to safeguard native biodiversity.

1. Introduction

Invasive alien plant species (IAPS) are defined as non-native species that cause negative impacts, economically, environmentally, or ecologically, on the habitats into which they have been introduced, whether intentionally or unintentionally, and beyond their historical range of distribution (Masters & Norgrove, 2010). IAPS are among the leading drivers of biodiversity loss globally, causing significant alterations to native ecosystems, displacing indigenous flora, and affecting ecological functions (Pyšek et al., 2020; Vilà et al., 2011; Dueñas et al., 2021; Reynolds & Aldridge, 2021). These species can significantly alter ecosystem structure and functioning by affecting native biota and abiotic conditions, including soil properties and microbial associations, often leading to the displacement of native flora and fauna (Kariyawasam et al., 2019; Reynolds & Aldridge, 2021). In Europe, for instance, IAPS are considered the second greatest threat to protected areas (Bradshaw et al., 2021). Such disruptions compromise habitat integrity and reduce the availability of essential ecosystem services (Gentili et al., 2021; Peter et al., 2021; Szumańska et al., 2021). Apart from these, IAPS have far-reaching negative impacts on agriculture, forestry, ecosystem services, and human health, ultimately resulting in substantial economic losses (Kim et al., 2021; Gentili et al., 2021; Peter et al., 2021; Szumańska et al., 2021). These economic burdens stem not only from the direct damage caused by invasive species but also from the significant costs associated with their prevention, control, and management (Richardson & Pyšek, 2007). For example, Australia has incurred at least US$298.58 billion (AU$389.59 billion) in losses and management expenses related to invasive species since the 1960s (Bradshaw et al., 2021). The ecological consequences of IAPS are particularly severe in biodiverse and fragile ecosystems such as those in mountainous regions and protected areas (Chaudhary et al., 2020). In the Eastern Himalayan region, characterized by high endemism and ecological sensitivity, the introduction and proliferation of

IAPS are increasingly documented as pressing conservation challenges (Singh, 2021; Tsering et al., 2019).

Bhutan, despite its strong conservation ethos and extensive protected area network, is not immune to the spread of IAPS (Thiney et al., 2019; Dorjee et al., 2020). Bhutan's diverse ecosystems, spanning from subtropical lowlands to alpine zones provide favorable conditions for the establishment and spread of invasive species (Thiney et al., 2019). Bhutan is home to a total of 964 alien plant species, classified under 545 genera and 139 families. Of these, 626 species are confined to cultivation, while the remaining 388 occur spontaneously in the wild—comprising 131 casuals (39%), 103 naturalized species (31%), and 101 invasive species (30%) (Dorjee et al., 2020; Tshering & Rinchen, 2025). A comprehensive literature review by Tshering and Rinchen (2025) listed 136 IAPS in Bhutan, including 22 major IAPS and 25 species with notable ecological impacts. Among these, nine species are listed among the world's 100 worst invasive alien species (IUCN, 2025). The most represented plant families were found to be Fabaceae (24 species), Rosaceae (20), and Asteraceae (19). In terms of growth forms, the majority of IAPS were herbs (73 species), followed by grasses (23) and trees (15).

Studies have reported the occurrence and increasing spread of species such as *Chromolaena odorata*, *Ageratina adenophora*, *Bidens pilosa*, and *Lantana camara* in lowland and mid-elevation zones of the country (Thinley et al., 2019). IAPS in Bhutan are predominantly found in disturbed habitats including roadsides, fallow lands, cultivated fields, as well as along the edges of wetlands and forested areas (Tshering & Rinchen, 2025). Studies have reported that IAPS, along with the effects of climate change, have begun to colonize highland pastures in the country, impeding the regeneration of native fodder grasses and thereby threatening traditional grazing systems (Thiney et al., 2019; Thinley et al., 2022). Similarly, in the subtropical regions of the country, grassland conditions have deteriorated over the years due to increasing invasion by IAPS (Wangmo et al., 2018).

In the face of these emerging threats, there remains a critical need for extensive and systematic studies to assess the ecological and economic impacts of IAPS in Bhutan, particularly to quantify the losses incurred and guide effective management interventions (Tshering & Rinchen, 2025). However, systematic assessments in protected areas, especially in remote and biologically rich landscapes like Jigme Singye Wangchuck National Park (JSWNP), remain limited. This study aims to address this knowledge gap by assessing the distribution, abundance, and potential ecological implications of IAPS within JSWNP, thereby informing future management and conservation strategies.

2. Materials and methods

2.1. Study area

The study was conducted in JSWNP, which is centrally located and plays a pivotal role in connecting the country's conservation landscapes in all four directions (Fig. 1). The park shares its southern boundary with Royal Manas National Park (RMNP) and is linked to Wangchuck Centennial National Park (WCNP) and Jigme Dorji National Park (JDNP) to the north through Biological Corridor (BC 8) and BC 2 respectively. To the southwest and east, it connects with Phibsoo Wildlife Sanctuary (PWS) and Phrumshingla National Park (PNP) via Biological Corridors 3 and 4, respectively. Spanning an area of 1,730 km², JSWNP is the third-largest protected area in Bhutan. It was officially designated as a national park in 1993 and became operational in 1995 (JSWNP, 2014).

The park's altitudinal gradient, ranging from approximately 250 meters above sea level (masl) in the southern foothills to 4,925 masl at the summit of Jowo Durshing, contributes to a rich mosaic of vegetation types, from subtropical forests to alpine meadows, supporting a wide range of habitats and high species diversity. It harbors over 55 species of mammals, 323 bird species, 376 butterfly species, 16 species of fish, and more than 42 species of herpetofauna (JSWNP, 2021). Several of these are globally threatened and of high conservation priority, including the Bengal tiger (*Panthera tigris tigris*), musk deer (*Moschus chrysogaster*), red panda (*Ailurus fulgens*), golden langur (*Trachypithecus geei*), Himalayan black bear (*Ursus thibetanus*), gaur (*Bos gaurus*), White-bellied heron (*Ardea insignis*), and Rufous-necked hornbill (*Aceros nipalensis*). Owing to its central location, JSWNP serves as an essential ecological corridor, facilitating wildlife movement between Bhutan's northern and southern protected landscapes (Letro, 2018).

The park's multiple-use zones along its periphery are home to 601 households and a population of approximately 5,538 people (Fig. 2). Among them are culturally significant indigenous groups such as the Monpa and Olep communities. These communities represent some of Bhutan's earliest settlers, and their unique cultural and linguistic heritage is under threat; JSWNP plays a critical role in safeguarding these traditions (Letro & Wangchuk, 2016; JSWNP, 2021).

The park, like any other protected areas in the country, is managed under a scientifically prepared conservation management plan with validity of 10 years. The current plan, effective from January 2022 to December 2031, identifies IAPS as one of the major conservation challenges facing the park (JSWNP, 2021). Their spread poses a serious threat to native biodiversity, alters habitat structure, and diminishes the quality of grazing lands critical for both domestic livestock and wild herbivores. If left unmanaged, IAPS can severely compromise ecosystem functions and conservation efforts within the park. In addition to IAPS, other threats highlighted in the management plan include human-wildlife conflict (HWC), poaching, illegal timber extraction, forest fires, unmanaged waste, drying water sources, and general habitat degradation.

Geologically, the park lies within a relatively young and rugged mountain system dominated by Pre-Cambrian and early Paleozoic quartzite and gneiss formations, interspersed with patches of sedimentary rocks such as limestone, dolomite, sandstone, and shale. The soils are predominantly clayey loam, offering good permeability and moderate moisture retention capacity (JSWNP, 2014; JSWNP, 2021).

2.2. Survey design

The study comprised 16 transects distributed across all four administrative ranges of JSWNP, encompassing traditional footpaths, cattle tracks and modern road networks. In the Taksha range, transects TPRO_01, TPRO_02, and TPRO_03 traversed the traditional foot trail from Phobjikha to Taksha via Rukha, while TPRO_04 followed the route from Zizi to Wangchekha, a traditional yak herding pasture. In the Langthel range, LPRO_01 followed the ancient trail from Langthel to Kudra via Jangbi and Phrumzur villages, and LPRO_02 covered Nabji to Kudra trail. In the Nabji range, NPRO_01 traced cattle tracks from Simkharka to Korphu-top; NPRO_02 followed the footpath from Gong to Reeti; NPRO_03 extended from Reeti to Relangthang (locally known as the GSI camp, referencing the Geological Survey of India's mining site); and NPRO_04 covered the entire route between Nabji and Relangthang. NPRO_05 followed the trail from Nimshong to Berti; NPRO_06 ran along the gewog road from Nimshong to the Korphu gewog office; and NPRO_07 covered the farm road between Nabji and Korphu villages. In the Tingtibi range, TbPRO_01 started from Chungshing village and extended halfway along the ancient trail to Berti, while TbPRO_02 completed the remaining section to Berti village. TbPRO_03 followed the farm road from Tingtibi town to Berti (Fig. 3).

Adaptive sampling methods have shown to enhance the effectiveness and efficiency of detecting and mapping the distribution of rare, spatially clustered populations compared to conventional sampling approaches (Acharya et al, 2000; Maxwell et al, 2012; Christman, 2000; Smith et al. 2004). The use of conventional systematic sampling often results in a low likelihood of selecting sampling units that contain the target rare species (Acharya et al, 2000). Given that most IAPS are distributed in cluster or randomly scattered patches, we employed an adaptive sampling approach. This involved establishing plots at fixed intervals along a transect, with additional opportunistic plots added when IAPS were encountered.

Starting from the initial point of each transect, sampling plots measuring 10 m x 10 m were established at regular 500-meter intervals, alternately on both sides of the transect. In addition to these systematically placed plots, opportunistic plots (10 m x 10 m) were laid whenever IAPS were encountered outside the predetermined intervals (Fig. 4).

2.3. Data collection

Data were collected from April to June 2020. Each transect was surveyed by a team of four to five observers, walking an average of 8 km per day. GPS units (eTrex 30) were used to measure distance and to mark the location of each subsequent plot. Within each plot GPS coordinates, altitude, slope, aspect, habitat type, IAPS species present, number of individuals, cover percent, and abundance ranking were recorded.

Percent cover was recorded using the Greater Yellowstone Area Cover Class: Low (< 5%), Moderate (5.1–25%), and High (25.1–100%). Abundance was ranked using the DAFOR scale: Dominant (D), Abundant (A), Frequent (F), Occasional (O), and Rare (R) (Smith et al, 2011). Each species observed within a plot was assigned a score from 0 to 5, corresponding to the categories: Rare (1), Occasional (2), Frequent (3), Abundant (4), and Dominant (5), with 0 indicating absence. These rankings were based on visual estimates of the species' relative coverage and frequency within each 10 m × 10 m plot.

2.4. Data analysis

RStudio (version 2022.07.2), MS Excel (version 2406) and QGIS (version 3.16.13) were used for data compilation, cleaning, organization and analysis (Fiske & Chandler, 2011).

Species richness was calculated as the total number of unique IAPS recorded within each transect, providing a measure of IAPS diversity across the landscape. Frequency was assessed by determining the proportion of plots in which each species was present, expressed as a percentage of the total number of surveyed plots. This approach allowed for identifying widely distributed species and evaluating the extent of their spread across the park.

To quantify dominance across the landscape, the mean and total DAFOR scores were calculated for each species. Additionally, the distribution of dominance rankings was summarized to highlight how often each species occurred within each abundance class, providing a landscape-level perspective on species dominance and spread.

Chi-square tests of independence were conducted separately for altitude and habitat types. Altitudes recorded at each plot were categorized into three classes: low (≤ 1000 m), mid (1001–2000 m), and high (> 2000 m). Habitat types were recorded in the field and treated as categorical variables representing various land cover and disturbance regimes. For each IAPS, plot-wise presence or absence was determined and cross-tabulated with the respective altitude class and habitat type to form contingency tables. Chi-square tests were then performed independently for each species to evaluate whether its occurrence was significantly associated with altitude or habitat. Species with insufficient data across classes were excluded from analysis to ensure test validity. Statistical analyses were conducted in the RStudio primarily utilizing the *"dplyr"* and *"readr"* packages for data wrangling, base R functions for statistical testing *"(chisq.test())"*, and the *"writexl"* package for exporting results to Excel for interpretation and reporting.

To explore patterns in IAPS composition across transects, a non-metric multidimensional scaling (NMDS) ordination was performed using the Bray-Curtis dissimilarity index. The input data consisted of abundance values of all 25 IAPS recorded across 16 transects. Prior to analysis, species abundance data were square-root transformed to reduce the influence of dominant species. This was done using the *"metaMDS()"* function from the *"vegan"* package in RStudio, with two dimensions (k = 2) and a maximum of 100 iterations to ensure convergence. Species vectors were fitted post hoc using *"envfit()"* to visualize directional influence of individual species in the ordination space.

Spatial distribution and invasion intensity of IAPS was analyzed using GPS coordinates and abundance rankings. Data were imported and processed in R using the *"sf"* package for spatial data management and *"ggplot2"* for visualization. Species-specific abundance data were transformed into spatial point layers, which were then subjected to kernel density estimation via *"stat_density2d()"* to generate hotspot maps. Bandwidth parameters were adjusted as necessary to accommodate species with limited sample sizes. The hotspot map was overlaid with the JSWNP boundary shapefile (projected to WGS 84 coordinate system) for spatial context. Similarly, hotspot map was generated for the most dominant IAPS, *Ageratina Adenophora*.

Minor edits were made to improve language clarity, readability, and grammar using ChatGPT, an AI-assisted copy-editing tool. All content was generated by the authors, who remain fully accountable for the final version of the manuscript.

3. Results

Total of 375 plots were laid across 16 transects, out of which 294 plots recorded the presence of one or more IAPS. Overall, a total of 25 unique IAPS were recorded from the park (Table 1) which included 4 of the world's worst 100 IAPS (IUCN, 2025; Tshering & Rinchen, 2025).

Table 1
List of IAPS recorded in JSWNP, including their common and local names, observed distribution within the park, associated ecological or socio-economic threats, and invasiveness status

Sl No	Species	Common/ Local name	Distribution in the park	Threats	Status
1	*Ageratina adenophora*	Croftonweed (Eng.)	Nimshong, Nabji, Korphu, Berti, Tongchur, Chungshing, Beyzam, Jangbi, Wangling, Phrumzur, Kudra, Oksengla, Simkharka, Reetey, Gong, GSI camp area, Radhithang, Dayu, Lawa, Lamga, Rukha, Migtena, Samthang, Harachu, Taksa.	Degrade pastureland, hazardous to animal and human health	Invasive alien
2	*Ageratum conyzoides*	Billy goat weed (Eng.); Elamey (Nep.); Rogpu-ngon (Sha.)	Nimshong, Berti, Kudra-Nabji trail, Zaichu, Tongsegang, Tongchur, Berti, Baybegang, Rawdung, Kezang-dra, Takabe, Wangdigang bridge area, Zhilingbe.	Reduce crop yield	Common dryland weed
3	*Alternanthera pungens*	Khaki weed (Eng.)	Takabe, Nabji (office compound)	Native plants	Invasive alien
4	*Amaranthus hybridus*	Smooth pigweeds (Eng.); Ludeyjhar (Nep.); Lasomo (Sha.)	Chungshing, Berti, Takabe	Agriculture crops	Common weed
5	*Amaranthus spinosus*	Spiny amaranth (Eng.); Naumoth (Dzo.); Ludeyjharkadey (Nep.)	Berti-top	Unpalatable, Agriculture; Widespread dryland weed	Invasive alien
6	*Bidens pilosa*	Blackjack (Eng.); Khaedu (Dzo); kuro (Nep.).	Nimshong, Korphu, Nabji, Wangdigang bridge area, Berti, Chungshing, Sangsangme, Kezangdra, Tongchur, Zhilingbe, Lawa,	Agriculture crops	Invasive alien

Sl No	Species	Common/ Local name	Distribution in the park	Threats	Status
			Lamga, Rukha, Migtena, Harachu.		
7	*Caesalpinia decapetala*	Mysore thorn (Eng.)	Gedu-zam	Native plants	Native invasive
8	*Chromolaena odorata*	Siam weed (Eng.); Achame (Nep.); nayra-ngon (Sha.)	Along Nimshong-Berti trail, Berti, Kezang-dra, Phrumzur, Jangbi, Wangdigang bridge area, Dayu, Rukha, Lawa, Lamga, Harachu, Samthang, Taksa.	Plant displacement, Reduces regeneration of trees.	Alien Invasive (World's worst IAS)
9	*Commelina benghalensis*	Spreading dayflower (Eng.); Kaney jhar (Nep.); Humbatenang (Sha.)	Berti	Agriculture crops; Common weed of lowland areas	Native invasive
10	*Conyza floribunda*	Horse weed/ Asthma weed (Eng.)	Sengling-brag, Zhilingbe.	Agriculture crops	Invasive alien
11	*Crassocephalum crepidioides*	Redflower ragleaf (Eng.); Dhadungphuley (Nep.)	Tongchur, Berti, Baybethang, Zhilingbe, Kezang-dra	Native plants	Common weed
12	*Dioscorea bulbifera*	Air potato (Eng.)	Berti, Takabe, along Berti - Chungshing trail	Forest (displace native plants)	Native invasive
13	*Imperata cylindrica*	Cogon grass (Eng.); Becho (Dzo.); Khar, Sirru (Nep.)	Takabe, Berti (eco-lodge area, Nabji (office compound)	Crops, native plants	Major invasive in country. (World's worst IAPS)
14	*Leucaena leucocephala*	Leaucana (Eng.); Tsashing (Dzo.)	Taksa (Range office compound).	Native plants	Major invasive (World's worst IAPS).
15	*Mikania micrantha*	Bitter vine (Eng.); Titaylaharo (Nep.)	Nimshong-Berti trail, Berti, Wangdigang bridge area, Chakharthang, Zhilingbe, Tongchur, Dayu, Lawa, Lamga.	Agriculture crops, forest, plantations	Major invasive in country. (World's worst IAPS)

Sl No	Species	Common/ Local name	Distribution in the park	Threats	Status
16	*Mimosa pudica*	Sensitive plant (Eng.)	Wangdigang bridge area and Takabe.	Agriculture crops, native plants	Major invasive
17	*Opuntia vulgaris*	Pickly pear (Eng.); Gewringa (Dzo)	Ugyen dra	Native plants, animal	Major invasive
18	*Oxalis latifolia*	Sorrel (Eng.)	Sengling-brag, Korphu, Gong, Reti-Gong trail, Reti, Radhithang, Zaichu, Kezang-dra.	Plants	Invasive
19	*Parthenium hysterophorus*	Parthenium weed (Eng.), Dushing (Dzo)	Sengling-brag, Rimtigang, Taksa, Rawdung, Wangdigang bridge area, Takabe, Zhilingbe.	Agriculture crops, animal and human health	Major invasive
20	*Pennisetum clandestinum*	Kikuyu grass (Eng.)	Radhitahng, Zhilingbe	Agriculture, forest, pasturelands	Major invasive
21	*Sida acuta*	Sida (Eng.); Balu jhar, Cannaino, Jaharu, Khareto (Nep.)	Baybegang, Zaichu, Berti, Takabe, Kezang dra, Rawdung, Tongchur, Wangdigang bridge area, Zhilingbe.	Pasturelands, rangelands	Major invasive
22	*Solanum viarum*	Tropical soda apple (Eng.)	Sengleng-brag, Shomgang, Reti, Radhithang, Tanbang, Chungshing area, Sangsangme, Claimchen, Zaichu, Tongchur, Berti, Baybegang.	Agriculture crops, forest, pastureland	Common weed
23	*Trifolium repens*	White clover (Eng.)	Jongkhey base, Khebethang, Neykhey, Wangche.	Native plants	Major invasive
24	*Verbascum thapsus*	Common mullein (Eng.)	Nabji-Korphu eco-trail, Jangbi	Native plants, pasturelands	Weed
25	*Xanthium strumarium*	Common cocklebur (Eng.)	Dayu, Rukha, Taksa	Agriculture crops, native	Occasionally dominant

Sl No	Species	Common/ Local name	Distribution in the park	Threats	Status
				plants	

3.1. Species richness by transect

Species richness, calculated as the total number of IAPS recorded per transect, varied across the surveyed areas. The highest richness was observed in transect TbPRO_03 with 17 species, followed by TbPRO_02 (13 species), NPRO_07 (11 species), and both NPRO_05 and TPRO_03 (10 species each). TPRO_01 and TPRO_04 recorded the lowest richness with only one species each (Fig. 5).

3.2. Frequency

Analysis of species frequency across all 375 plots revealed that *Ageratina adenophora* occurred in approximately 64% of surveyed plots. Other recorded frequencies were *Solanum viarum* (15.47%), *Bidens pilosa* (13.07%), *Chromolaena odorata* (10.67%), *Mikania micrantha* (8.80%), and *Oxalis latifolia* (8.80%). In contrast, *Opuntia vulgaris*, *Mimosa pudica*, *Xanthium strumarium*, and *Leucaena leucocephala* were each recorded in fewer than 1% of plots (Fig. 6).

3.3. Dominance, based on DAFOR scale

Abundance ranking based on the DAFOR scale revealed *Ageratina adenophora* as the most dominant IAPS across the surveyed plots. It was recorded most frequently at Rank 3 (Frequent, n = 84) and Rank 4 (Abundant, n = 77), with substantial occurrences at Rank 2 (Occasional, n = 49) and Rank 1 (Rare, n = 35). It was also recorded at Rank 5 (Dominant, n = 5). Other species such as *Solanum viarum*, *Bidens pilosa*, *Chromolaena odorata*, and *Mikania micrantha* also occurred across higher abundance ranks. Species including *Crassocephalum crepidioides*, *Parthenium hysterophorus*, *Sida acuta*, and *Trifolium repens* were observed mostly at lower ranks (1–2), while *Opuntia vulgaris*, *Mimosa pudica*, and *Leucaena leucocephala* were rarely recorded (Fig. 7).

3.4. Association of IAPS with altitude and habitat type (Chi-square tests)

Chi-square tests showed significant associations between several IAPS and both altitude classes and habitat types. *Ageratina adenophora* showed highly significant relationships with altitude ($\chi^2 = 44.38$, df = 2, $p < 0.001$) and habitat type ($\chi^2 = 46.45$, df = 13, $p < 0.001$). *Sida acuta*, *Mikania micrantha*, *Ageratum conyzoides*, and *Trifolium repens* were also significantly associated with both altitude and habitat. Species including *Bidens pilosa*, *Oxalis latifolia*, *Conyza floribunda*, *Solanum viarum*, *Chromolaena odorata*, *Crassocephalum crepidioides*, *Imperata cylindrica*, *Amaranthus hybridus*, and *Mimosa pudica* were significantly associated with altitude only, while *Pennisetum clandestinum*, *Dioscorea bulbifera*, and *Alternanthera pungens* were significantly associated with habitat type only (Table 2).

Table 2
Result of the chi-square (χ^2) tests of independence (IAPS vs. altitude and Habitat types)

Species	χ^2 Altitude	DF Altitude	P_value Altitude	χ^2 Habitat	DF Habitat	P_value Habitat
Ageratina adenophora	44.381	2	2.3E-10	46.449	13	1.2E-05
Bidens pilosa	7.895	2	1.9E-02	63.738	13	1.1E-08
Oxalis latifolia	11.444	2	3.3E-03	29.896	13	4.9E-03
Sida acuta	47.172	2	5.7E-11	94.394	13	2.0E-14
Conyza floribunda	11.859	2	2.7E-03	34.303	13	1.1E-03
Parthenium hysterophorus	11.181	2	3.7E-03	15.022	13	3.1E-01
Solanum viarum	11.726	2	2.8E-03	57.402	13	1.5E-07
Chromolaena odorata	87.276	2	1.1E-19	27.571	13	1.0E-02
Mikania micrantha	90.932	2	1.8E-20	82.663	13	3.5E-12
Ageratum conyzoides	90.111	2	2.7E-20	92.341	13	5.0E-14
Trifolium repens	189.997	2	5.5E-42	128.831	13	3.6E-21
Crassocephalum crepidioides	37.044	2	9.0E-09	46.860	13	1.0E-05
Verbascum thapsus	0.278	2	8.7E-01	0.649	13	1.0E + 00
Pennisetum clandestinum	0.559	2	7.6E-01	53.253	13	8.2E-07
Caesalpinia decapetala	4.230	2	1.2E-01	0.649	13	1.0E + 00
Leucaena leucocephala	4.230	2	1.2E-01	0.649	13	1.0E + 00
Imperata cylindrica	8.161	2	1.7E-02	38.073	13	2.8E-04
Dioscorea bulbifera	1.255	2	5.3E-01	28.363	13	8.1E-03
Amaranthus hybridus	21.064	2	2.7E-05	72.364	13	2.9E-10
Amaranthus spinosus	4.230	2	1.2E-01	0.649	13	1.0E + 00
Xanthium strumarium	4.230	2	1.2E-01	0.649	13	1.0E + 00
Alternanthera pungens	5.500	2	6.4E-02	29.732	13	5.1E-03
Mimosa pudica	8.161	2	1.7E-02	12.903	13	4.6E-01

Species	χ² Altitude	DF Altitude	P_value Altitude	χ² Habitat	DF Habitat	P_value Habitat
Commelina benghalensis	1.255	2	5.3E-01	21.317	13	6.7E-02

3.5. Ordination (NMDS)

The NMDS ordination (stress = 0.063; 2 dimensions) revealed distinct patterns in IAPS composition across the 16 transects in JSWNP. Transects such as TPRO_01 and TPRO_04 were spatially isolated in the ordination space, indicating a unique or low density of IAPS. In contrast, transects like TPRO_03, TbPRO_02, TbPRO_03 NPRO_05, and NPRO_07 clustered closely, suggesting similar species composition and higher IAPS richness. The species vectors indicated that *Ageratina adenophora*, *Solanum viarum*, *Parthenium hysterophorus*, and *Sida acuta* were major contributors to dissimilarity in community composition. For instance, *Ageratina adenophora* was strongly associated with transects on the right-hand side of the plot, while *Trifolium repens* was associated with more isolated transects like TPRO_01 and TPRO_04 (Fig. 8).

3.6. IAPS Hotspot mapping

The combined heatmap of all recorded IAPS revealed extensive invasion zones, primarily concentrated in the southeastern lowland valleys of JSWNP, particularly within the Tingtibi and Nabji ranges. Moderate invasion intensity was also observed in the southwestern region, represented by the Taksha range (Fig. 9). Among the recorded species, *Ageratina adenophora* exhibited the most widespread and intense invasion, forming dense clusters across both southern and central parts of the park (Fig. 10).

4. Discussions

This study provides the first systematic and spatially comprehensive assessment of IAPS in JSWNP, revealing interesting patterns of species richness, frequency, dominance, and spatial distribution. The findings point to the growing ecological threat posed by IAPS to native biodiversity, habitat quality, and ecosystem function in the national park.

Ageratina adenophora emerged as the most dominant and widely distributed IAPS, occurring in over 60% of sampled plots and exhibiting strong associations with multiple habitat types and elevation zones. This is consistent with global studies that categorize the Himalayan region including Bhutan under high risk area of *A. Adenophora* invasion (Changjun et al, 2021) and regional studies that reported an alarming 87.5% invasion by *A. Adenophora* in western Bhutan (Sherub & Dawa, 2022). Its dominance across various DAFOR ranks, particularly in frequently and abundantly invaded plots, highlights its ecological plasticity and aggressive colonization behavior.

A. *adenophora* is considered one of the most aggressive and problematic invasive species across Asia, Africa, and Oceania (Tang et al., 2019). The invasive success of *A. adenophora* can be attributed to a combination of ecological and biological traits. Notably, the species exhibits prolific reproductive capabilities, both sexually and asexually (Feng, 2008). A single ramet is capable of producing up to 10,000 seeds per growing season, with 15–30% of them being viable (Parsons & Cuthbertson, 2001). These seeds exhibit discontinuous germination, enhancing their longevity in the soil (Shen et al., 2011). Their small size facilitates effective dispersal via wind and water, enabling both short- and long-distance spread (Wang et al., 2011). In addition to its reproductive advantages, *A. adenophora* exerts strong allelopathic effects, suppressing the growth of native plant species (Zhong et al., 2007). The species also alters soil microbial communities in ways that hinder native species regeneration while promoting its own establishment and persistence (Niu et al., 2007; Xu et al., 2012). High tolerance to environmental stress (Rivera et al., 2017) and pronounced morphological plasticity (Zhao et al., 2013; Shen, 2019) further enhance its adaptive capacity across diverse habitats.

The NMDS ordination further supported these findings by revealing distinct compositional patterns among transects. TPRO_01 and TPRO_04, which appeared spatially isolated in the ordination space, were characterized by low IAPS richness and unique species composition, suggesting minimal invasion or the presence of a different assemblage. In contrast, TPRO_03, TbPRO_02, TbPRO_03, NPRO_05, and NPRO_07 formed a tight cluster in the ordination, indicating high similarity in IAPS composition, likely influenced by similar disturbance regimes or environmental conditions. The species vectors identified *Ageratina adenophora*, *Solanum viarum*, *Parthenium hysterophorus*, and *Sida acuta* as key drivers of dissimilarity, reinforcing their dominant roles in shaping community structure across invaded sites.

According to Wan & Wang (2018), rising temperatures caused by climate change are creating increasingly favorable conditions for the establishment and spread of IAPS particularly in higher elevations and latitudes. Human activities such as road expansion further facilitate the movement of IAPS into previously undisturbed and remote areas by creating dispersal corridors (Wang, et al., 2017). Similarly, international trade plays a significant role in the unintentional introduction of invasive species across borders (Bertelsmeier et al., 2015). In JSWNP, species richness was highest in the southern lowland valleys, notably in the Tingtibi and Nabji ranges, where a hot and humid climate, coupled with road networks and human settlements, likely creates favorable conditions for invasion. Transects such as TbPRO_03, TbPRO_02, and NPRO_07 recorded the highest diversity of IAPS, suggesting that these areas function as invasion hotspots. Conversely, upper elevation transects such as TPRO_01 and TPRO_04 recorded minimal IAPS presence, suggesting elevation acts as a natural barrier to some extent, though the upward migration of species like *Trifolium repens* and *Ageratina adenophora* warrants concern under changing climatic conditions.

The results of chi-square analyses confirm that many IAPS exhibit significant habitat and elevation preferences. Species such as *Mikania micrantha*, *Chromolaena odorata*, and *Sida acuta* demonstrated strong associations with specific habitat types and altitudinal zones, suggesting that environmental filtering plays a role in shaping IAPS assemblages. These patterns provide valuable insight for predicting future invasion dynamics under changing land use and climate regimes.

The spatial hotspot maps further reinforced these patterns, identifying high-density clusters of IAPS, particularly in the southeastern and southwestern regions of the park. The widespread distribution and intensity of *Ageratina adenophora* invasion is especially alarming, given its known impacts on native vegetation and grazing systems. These maps are critical tools for visualizing invasion pressure and prioritizing site-specific management interventions.

Management recommendations

In light of these findings, several key recommendations are proposed to guide the effective management of IAPS within JSWNP:

Targeted control in invaded hotspots: Immediate efforts should focus on high-density invasion zones identified in southeastern and southwestern JSWNP, particularly within the Tingtibi and Nabji ranges. Mechanical removal, combined with community-based monitoring, has proven effective in restoring IAPS-invaded habitats (Venette et al, 2021).

Species-specific integrated management strategies: The park should prioritize immediate control of dominant species, especially *A. adenophora*, using integrated methods such as manual removal and prescribed burning. Manual and fire-based removal strategies have been successfully implemented in Southwest China, where these techniques reduced *A. adenophora* cover by over 70% within two years (Wang & Wang, 2006).

Early detection and rapid response (EDRR): Species with limited distribution (e.g., *Opuntia vulgaris*, *Leucaena leucocephala*) should be subject to early eradication to prevent further establishment and spread. Preventing the invasion of IAPS into new suitable regions is the most effective and cost-efficient strategy to avoid ecological and economic damage (Keller et al., 2008). Establishing sentinel monitoring sites and community-supported early warning systems can significantly increase detection rates (Pocock et al, 2024 ; Lovell-Read et al, 2023).

Community engagement and education: The involvement of local communities, particularly those residing in high-risk areas, is critical. Awareness programs should highlight the impacts of IAPS on livelihoods, traditional grazing lands, and ecosystem services, and promote active participation in monitoring and removal activities. Engaging local communities in surveillance, species identification, and control fosters collective stewardship. Community-based programs in Nepal, relying on focus-group discussions, have revealed that locals can prioritize and manage IAPS effectively without extensive external support (Shrestha et al., 2019; Pocock et al, 2024).

Policy and cross-sectoral integration: Coordination with local governance bodies and integration of IAPS management into development planning (e.g., road construction, agriculture) can minimize anthropogenic dispersal pathways.

Long-term monitoring and research: Establishing a standardized IAPS monitoring framework and expanding research into species ecology, dispersal mechanisms, and climate interactions is essential for adaptive management. Scientific evidence on species ecology and invasion pathways is essential for informed decision-making and priority setting.

This study provides a critical baseline for understanding IAPS dynamics in one of Bhutan's most ecologically significant protected areas. The spatial and ecological insights generated here can inform broader national strategies for invasive species control and contribute to the preservation of Bhutan's unique biodiversity and ecological resilience.

Although the data were collected in 2020, the findings from this study provide the most recent systematic baseline on the distribution and composition of IAPS within JSWNP. Given the increasing pressures from land-use change and climate variability, these findings remain highly relevant for guiding current and future management efforts with respect to IAPS.

5. Conclusion

This study presents the first comprehensive assessment of IAPS in JSWNP, revealing concerning patterns of species richness, distribution, and ecological dominance. The findings highlight the growing threat posed by IAPS, particularly *Ageratina adenophora*, to native biodiversity, ecosystem functioning, and traditional land-use systems. The significant associations between IAPS occurrence and specific altitudinal zones, habitat types, and human disturbances emphasize the combined influence of environmental and anthropogenic factors in driving invasion patterns. Additionally, the identification of spatial hotspots offers valuable guidance for prioritizing control and restoration efforts. As Bhutan continues to experience ecological pressures from climate change and land-use changes, timely and evidence-based management of IAPS in protected areas such as JSWNP is essential. This study provides a strong foundation for informed conservation planning, long-term ecological monitoring, and the development of integrated strategies to protect Bhutan's rich ecological heritage.

Declarations

Competing Interests

The authors have no relevant financial or non-financial interests to disclose. The management of JSWNP provided support and facilitation during the research but had no influence on the study design, data analysis, or manuscript preparation.

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Author Contributions

Both authors contributed to the conception and design of the study. The first author, Abir Man Sinchuri, was responsible for material preparation, data collection, analysis, drafting, and finalizing the manuscript. The second author, Phuentsho, contributed to study design, data collection, reviewing the initial draft, and proofreading the final version. All authors have read and approved the final manuscript.

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Figures

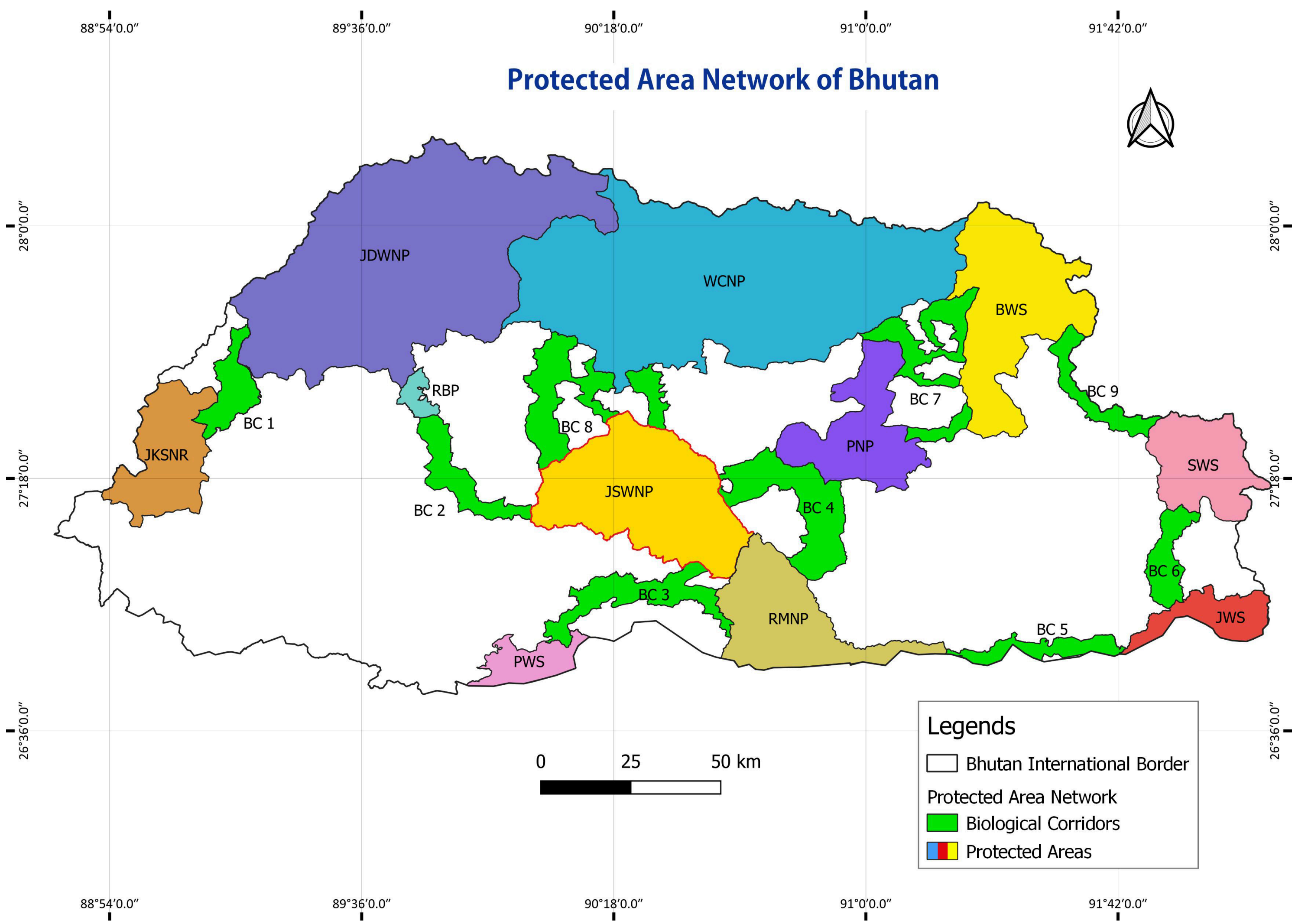

Figure 1

Protected area network map of Bhutan showing the strategic location of JSWNP as a connecting link between southern and northern conservation landscapes

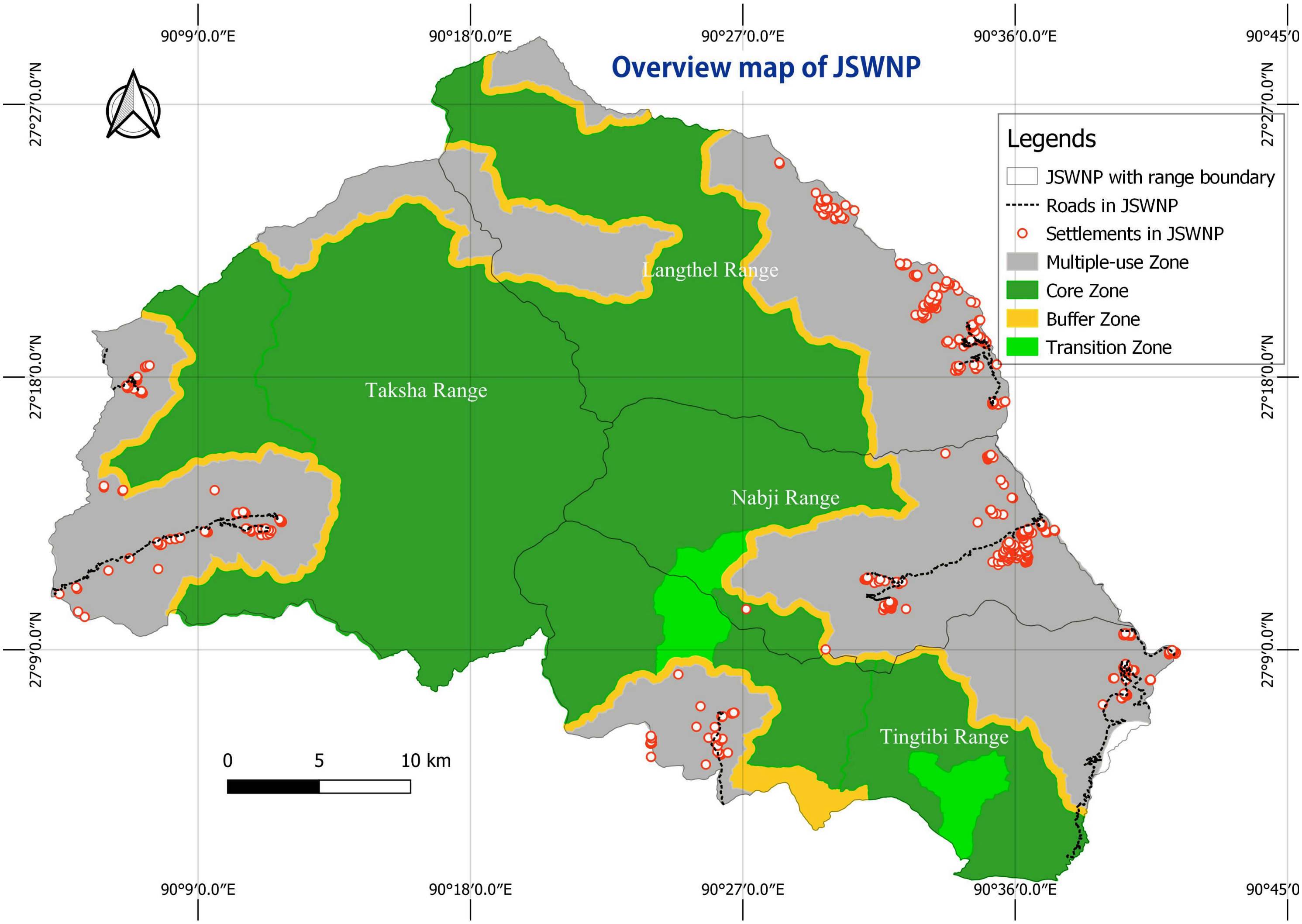

Figure 2

Overview of JSWNP showing the park's zonation, human settlements, road network and range boundaries

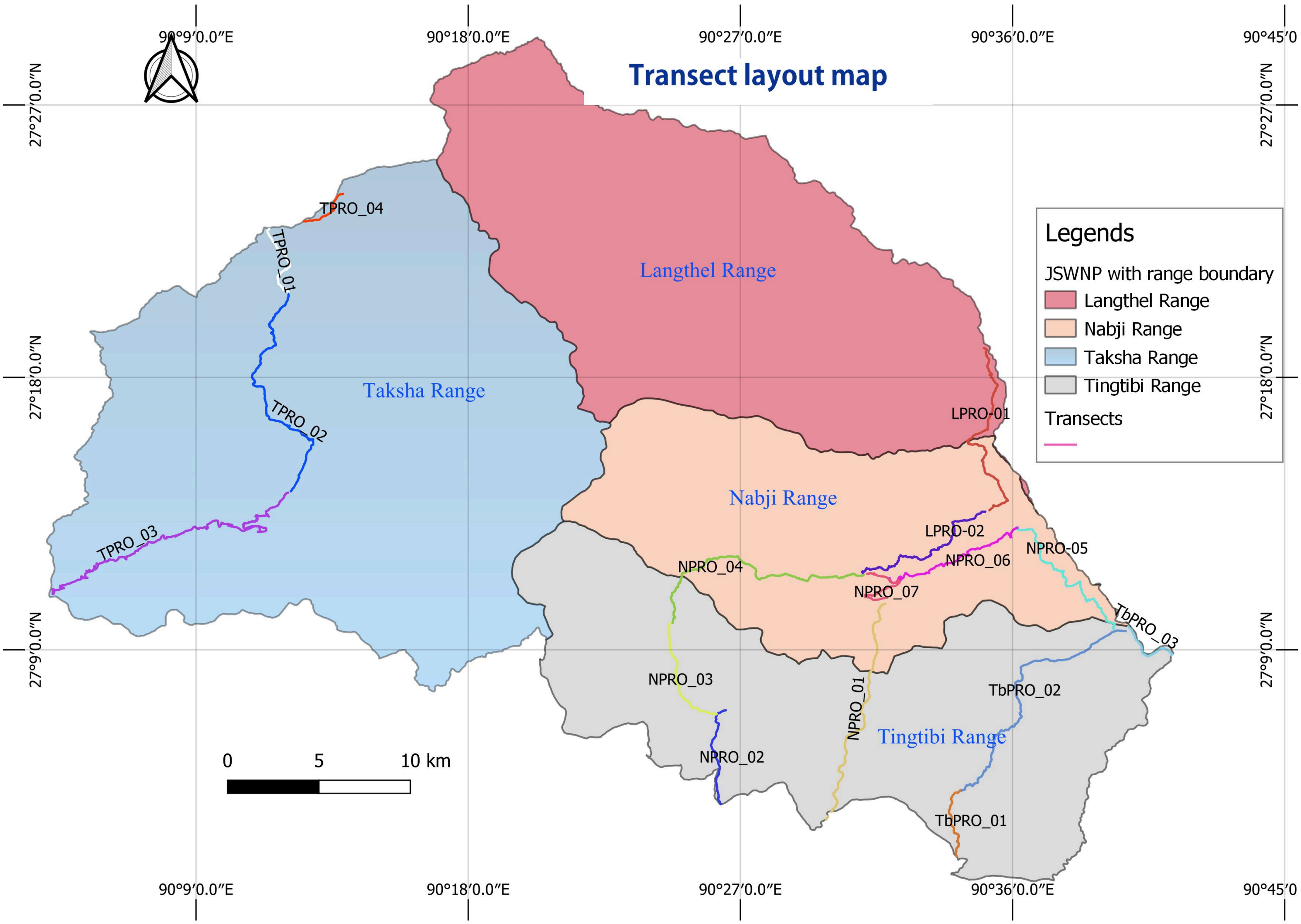

Figure 3

Transect layout map depicting the extent and spread of the 16 transects laid for this study. All these transects follow traditional foot-trails, farm roads, gewog roads or national highway falling inside JSWNP

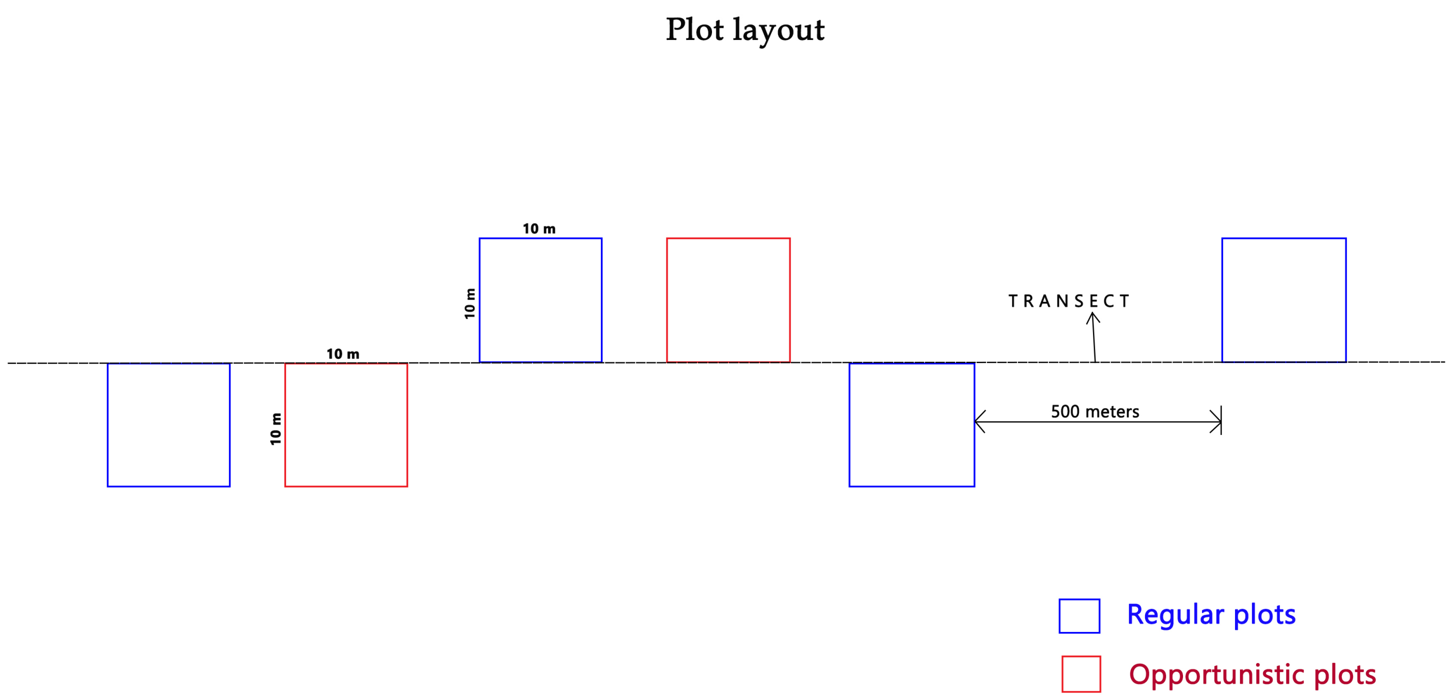

Figure 4

Diagrammatic representation of plot layout along the transect, showing the regular plots at 500m interval and opportunistic plots; both 10m x 10m. Created using Adobe Photoshop CS6

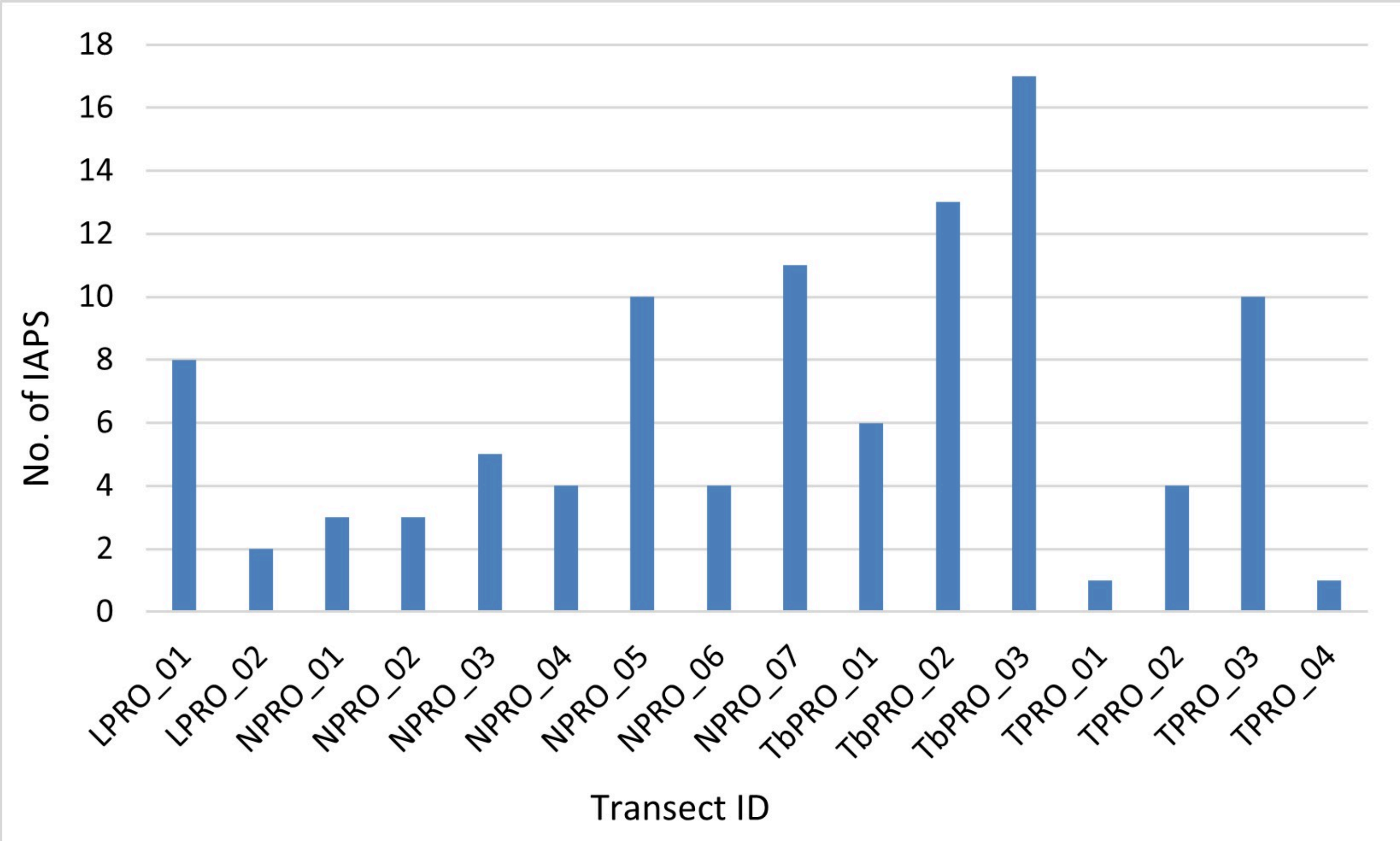

Figure 5

Species richness, plotted as the total number of IAPS recorded per transect

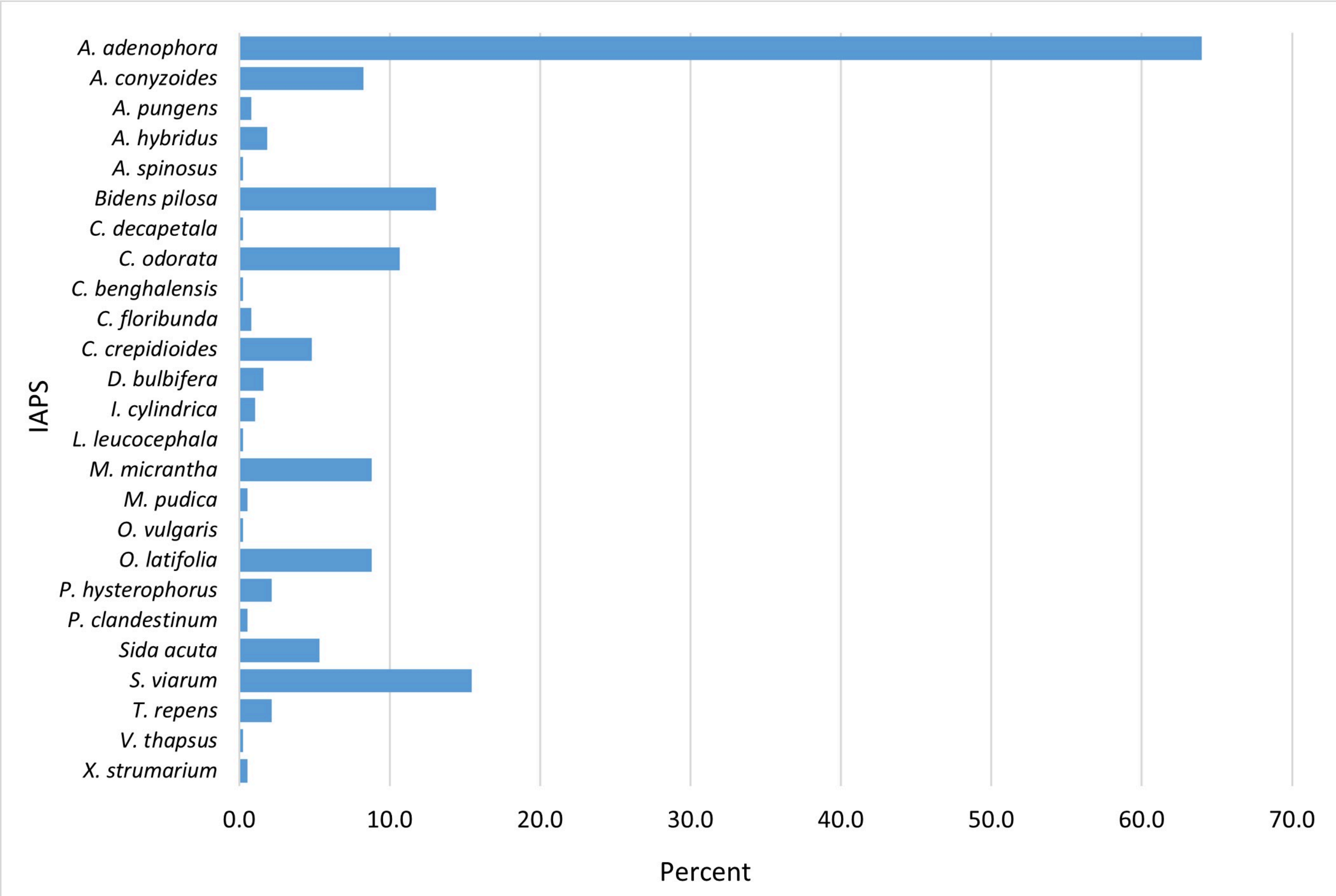

Figure 6

Frequency of each IAPS plotted as the percentage of plots each species was present showing A. adenophora as the most widespread species, present in 64% of plots

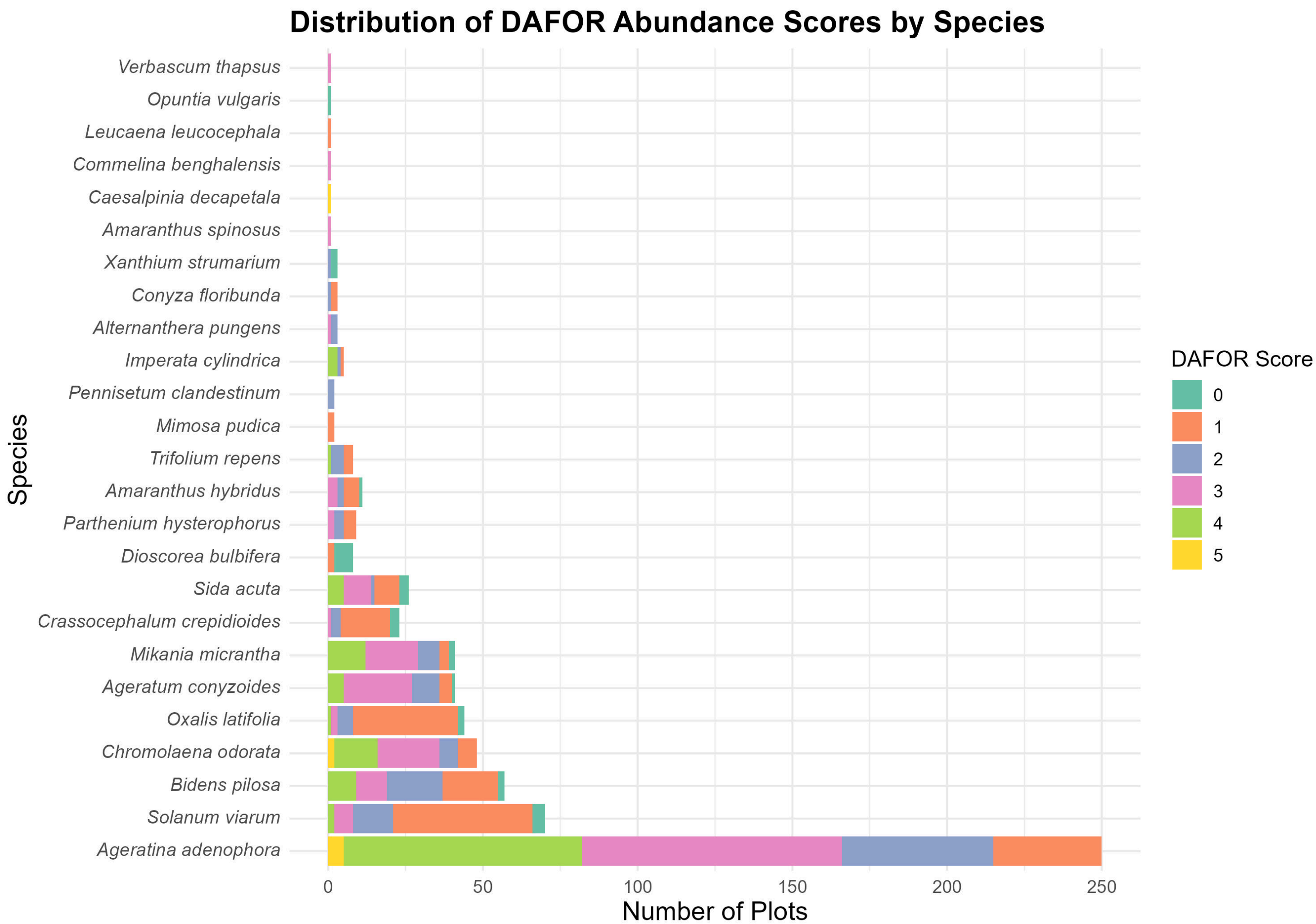

Figure 7

Species-wise distribution of DAFOR Abundance scores. Dominant (D) = 5, Abundant (A) = 4, Frequent (F) = 3, Occasional (O) = 2, Rare (R) = 1, and Absent = 0

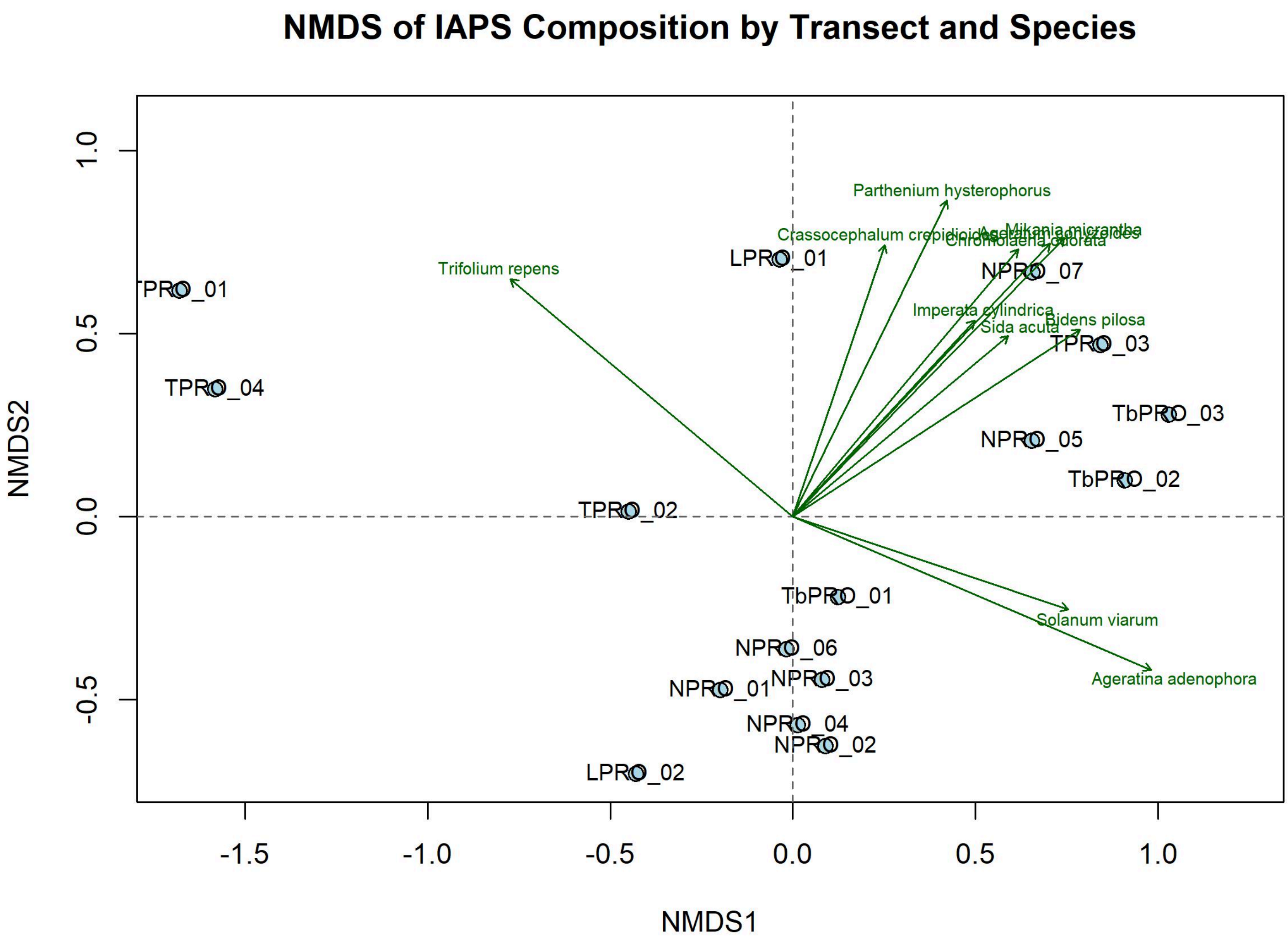

Figure 8

Non-metric multidimensional scaling (NMDS) ordination using Bray–Curtis dissimilarity index (stress = 0.063; 2 dimensions)

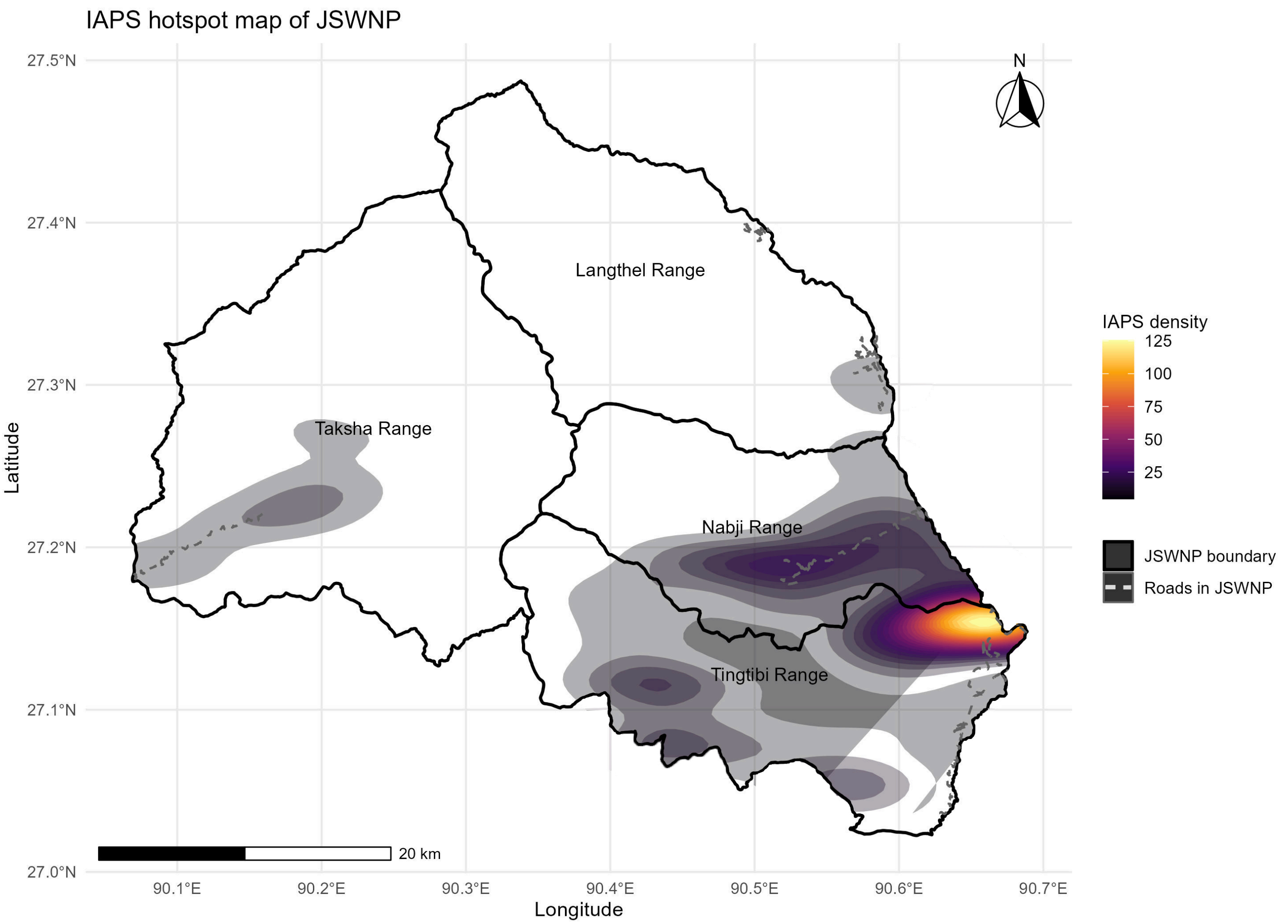

Figure 9

Hotspot map showing the spatial concentration of all 25 IAPS recorded in JSWNP.

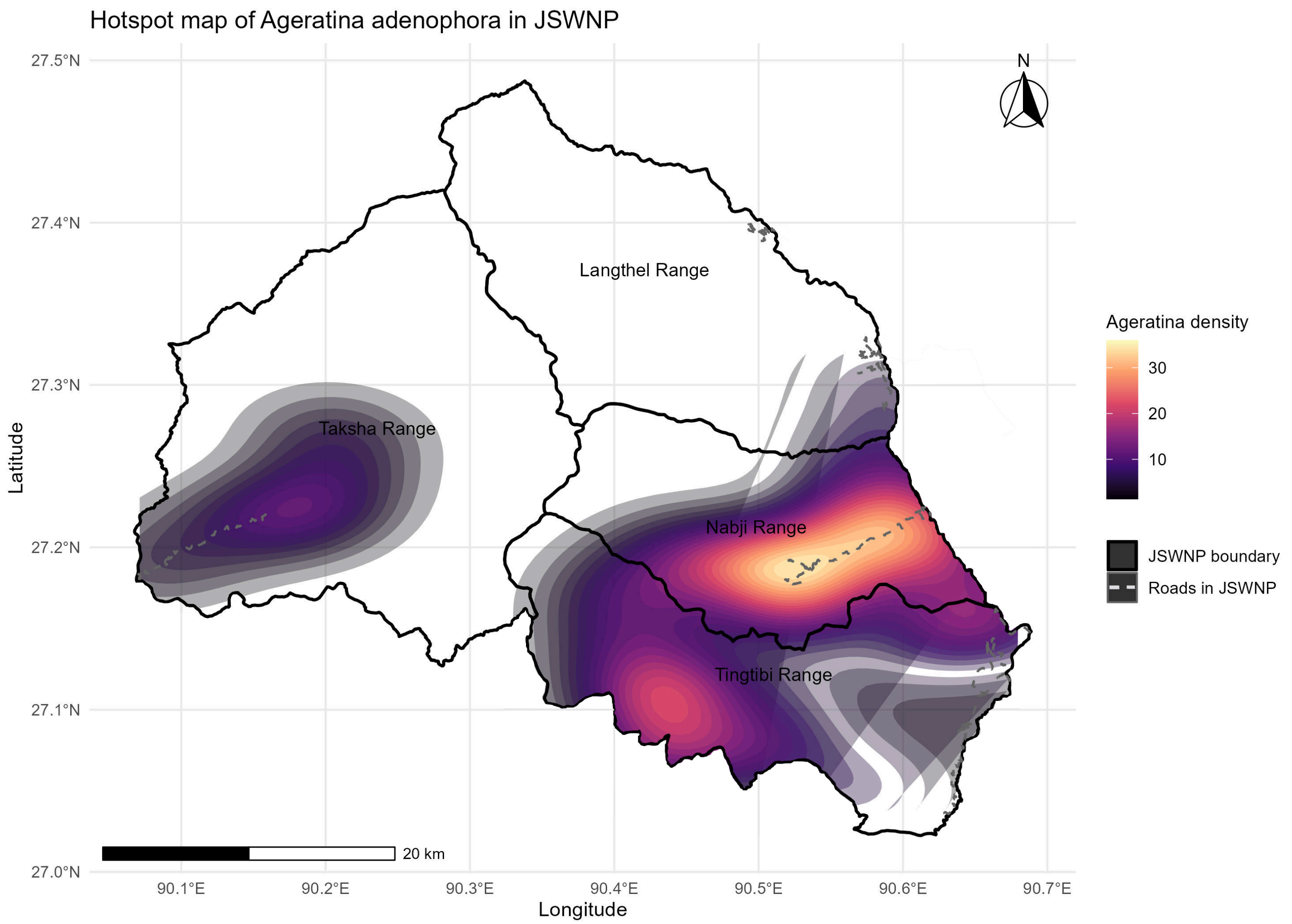

Figure 10

Hotspot map of A. adenophora, the most dominant IAPS of JSWNP.