

Review

Review of Invasive Plant Functional Traits and Management Using Remote Sensing in Sub-Saharan Africa

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Abstract: Biodiversity and sustainable development in Sub-Saharan Africa (SSA) are considerably impacted by invasive alien plants (IAPs). Increasing plant invasions in SSA threaten agricultural productivity, biodiversity conservation, and other socioeconomic activities, which in turn put the United Nations Sustainable Development Goals (SDGs) in peril. In order to effectively combat IAPs, understanding their functional traits (morphological, physiological, and phenological traits) and integrating them into remote sensing (RS) is vital. While functional traits influence IAPs' fitness to invade and establish in a new geographical range, RS aids in studying them remotely, delineating and mapping them, and predicting their potential invasions. The information on this study topic was gathered by reviewing various existing studies published between 2000 and 2024. Based on this review, it was deduced that the majority of IAPs are fast-growing (or acquisitive), with a shorter leaf lifespan, bigger leaves, and higher plant height, ultimately resulting in a higher resource acquisition ability. We established further that in SSA, there are limited studies on IAP functional traits and their integration in RS. Many studies conducted in the region focus mostly on IAP distribution. Evidence from prior studies revealed that functional trait remote sensing (FTRS)-based research not only improves detection and mapping but also predicts whether a certain alien plant can become invasive or expand its distribution range. Thus, using the FTRS approach could help IAP management in SSA, ultimately achieving the SDGs. Our review discusses IAP implications in SSA (e.g., Angola, Tanzania, Benin, Kenya, Uganda, Rwanda, Zambia, Burundi, Zimbabwe, Botswana, Malawi, etc.) and for the achievement of SDGs; functional traits and their impact on alien invasions; and the importance of incorporating functional traits into RS.

Keywords: aliens; biodiversity; conservation; ecosystem; functional diversity; invasion; plant traits; SDGs



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1. Introduction

Invasive alien plants (hereafter IAPs) are considered environmental pollutants because, like other pollutants, they are threatening human well-being and livelihoods [1,2], biodiversity, and natural ecosystems [3–5]. They cause biodiversity loss and functional changes [6,7], endangering and/or suppressing native (local or indigenous) species [3,8], and forming novel plant communities [1,9]. They are one of the major factors inducing biotic homogenization [9], which is defined by an increase in genetic, taxonomic, or functional similarities across different sites over a predetermined period of time [10,11]. They alter the community structure and composition of recipient environments by displacing or suppressing the abundance and/or species richness of native species [12,13]. A study conducted by Forey et al. [9] in a Fijian rainforest provides evidence in favor of this, showing that IAP *Pinanga coronata* (Blume) Blume decreased native species richness and Shannon diversity by 50% and 33%, respectively. Another study in southern Poland by Stefanowicz et al. [14] showed that IAP (*Solidago gigantea* Aiton) decreased soil microbe biomass

and microbial activity. Also, it was reported that IAPs can change the biocenotic conditions and life cycles of animals [12,15]. For instance, invasive moss (*Campylopus introflexus* (Hedw.) Brid) changed beetle feeding preference, spider hunting mode, and body size [12]. They added that in areas with moss invasion, the proportions of web-building spiders and phytophagous beetles were lower.

In addition to the loss of native flora and fauna species [16–18], the IAPs can also decrease the functional diversity of native plant [19,20] and fauna communities [12] leading to functional homogenization. Functional diversity can be defined as a measure of an organism's functional traits that affect one or more aspects of an ecosystem's functioning. It usually quantifies the abundance and dispersion of living things occupying a specific niche. Examples of functional diversity are functional divergence, evenness, and richness [19–21]. Considering plants, Tordoni et al. [21] found that the presence of alien plants decreased the functional diversity of the co-occurring native plant communities in coastal dunes, and similar results were found in other ecosystems [22–24], as well as in urban environments [25]. Another study revealed that moss invasion reduced the functional diversity of carabid beetles while increasing spiders' functional similarity [12]. This occurred along with the dramatic change in species composition, i.e., abundance, richness, and diversity [12], ecosystem structure [13], and the functioning of an invaded ecosystem [5,16,20]. Because of this, it is claimed that biological invasion is one of the major causes of biodiversity loss and changes in ecosystem services provision globally [4,18,20,26]. Nevertheless, the impacts of IAPs and biodiversity loss are deemed significant based on how species traits interact with the recipient environment [5,9].

In the last decades, many studies addressed plant invasion under a functional point of view, i.e., by measuring plant functional traits, which are defined as any morpho-physiological characteristics that impact plant fitness indirectly via their effects on growth, reproduction, and survival [27,28]. This approach allowed us to answer several questions related to plant invasion, from assessing the effects of IAP invasion on ecosystems structure and functionality [21,29] to highlighting the determinants of IAPs' invasiveness [30–32]. In particular, several studies performed multispecies comparison between native and/or non-invasive alien species vs. IAPs [30–32], revealing consistent patterns in traits differences between IAPs and native/non-invasive alien species, with some exceptions. Generally, the IAPs' ability to adapt to a variety of environmental conditions and disturbances, as well as their competitive capacity, enhance their invasiveness [8]. Indeed, in many cases, IAPs outperformed native plants in terms of traits related to growth, e.g., height, size, relative growth rate, leaf area, photosynthetic rates, etc., and reproduction, e.g., fecundity, seed number, germination rate [16,32–37]. However, despite the great number of studies and substantial meta-analytic efforts, a unique set of traits responsible for IAP invasion has not been identified to date. For instance, Daehler [30] found that growth rate, competitive ability, or fecundity did not differ between IAPs and native species, concluding that differences between the two groups of species often depend on growing conditions. Similar results were found in Mediterranean ecosystems [38–40], suggesting that invasion is a context-dependent process and that multiple suites of traits could promote invasiveness in different environments [32,40]. In this light, different hypotheses have been proposed to explain the success of IAPs. The “try harder” hypothesis [41] suggests that successful aliens deal better with the local conditions than resident species, expressing a set of functional traits different from those of native species. On the other hand, the “join the locals” hypothesis [41] predicts similarities among alien invasive and native species.

Another feature that might be associated with invasiveness in alien species is phenotypic plasticity [42,43], defined as the ability of an organism to develop different phenotypes under different environmental conditions [44]. A higher phenotypic plasticity could help IAPs to adjust and cope faster with new environments and eventually expand the distribution range and ecological niche [34,45]. However, only a few studies reported higher phenotypic plasticity in IAPs, while in others no differences between IAPs and native species were detected [43,46–48]. Besides functional traits, IAP invasion generally occurs when

niches become unoccupied due to disturbances that increase resource availability or when competitors and natural enemies reduce the performance of native species [4,49]. Anthropogenic pressure and elevation [8,18], and the absence of natural antagonists (e.g., natural enemies or predators) to suppress them, also foster their invasion [5,7,50].

Considering the deleterious impacts of IAPs on the environment, biodiversity, and global economy [3,17], there is a need for effective countermeasures for their invasions [51,52]. In Article 8(h), the Convention on Biodiversity Diversity (CBD) underlines preventing the introduction, management, or eradication of alien species that threaten habitats, ecosystems, or species [16]. Additionally, the UN Decade on Ecosystem Restoration, led by Resolution 73/284, seeks to stop, prevent, and reverse ecosystems' degradation on our planet caused by alien species (<https://www.decadeonrestoration.org/>, accessed on 27 November 2023). This can be effectively achieved through the integration of functional traits into remote sensing (RS). For instance, by detecting and utilizing high-resolution imagery and hyperspectral imaging, scientists can identify, monitor, and manage IAPs with unprecedented accuracy and efficiency. Furthermore, the use of a functional trait remote sensing (FTRS) research approach can further improve our knowledge of the dynamics, control, mechanisms, and impacts of alien invasions [53–55]. For studying alien invasions, RS is the most thorough and practical method available as it demonstrates great potential to detect functional traits in IAPs [56–61]. However, Sub-Saharan Africa (SSA) still has significant gaps in its application when it comes to studying and managing alien plant invasions.

Despite the increasing research on IAPs, most studies in SSA focus on the distribution of IAPs and a few functional traits, e.g., allelochemicals and chemical defenses that facilitate invasion [1,50,62–64]. In general, functional trait-based analyses on SSA IAPs are very scarce and have seldom been integrated into RS. As such, much less is known in SSA about how IAP functional traits play a role in plant invasions and the application of RS in invasion control. Since functional traits and RS are useful in mapping, predicting, and managing plant invasions [65–68], integrating them into research in SSA is important. It is noteworthy, however, that a combination of multiple traits—rather than a single trait—is crucial for a more accurate prediction of invasion of alien plants [17,69]. Because of the inadequate knowledge of IAPs' impact in developing countries, particularly in SSA, and limited FTRS-research in the region, this review paper discusses the (i) implications of IAPs in SSA and for the achievement of the United Nations Sustainable Development Goals (UN SDGs), (ii) functional traits and their impact on invasions, and (iii) importance of incorporating functional traits into RS; and lastly, it presents (iv) the lessons learned and ways forward.

2. Literature Review Method

The published peer-reviewed original and review research articles on biological invasions, specifically on IAPs, were retrieved from international scientific databases and publishers. These include Springer, Elsevier, Taylor & Francis, SAGE, Scopus, Wiley-Blackwell, PLOS ONE, Hindawi, MDPI, the Directorate of Open Access Journals, African Journal Online, and the Web of Science (Table 1). We reviewed one hundred and ten (110) articles focusing on biological invasions, alien species, plant functional traits, remote sensing, and the impacts of IAPs on biodiversity and the environment. We specifically looked for the words “invasive plants”, “alien species”, “plant invasion”, “biological invasion”, “plant traits”, “plant functional traits”, “allelopathy”, “allelochemicals”, “impact of invasive”, “biodiversity loss”, “mycorrhizal plants”, “UN SDGs”, “biological invasion in Sub-Sahara”, “functional diversity”, “remote sensing”, and “biological invasion and UN SDG” in the keywords, titles, and abstracts of the articles. We did not use pre-print articles and unpublished research materials.

Table 1. The number of literature sources that were processed.

Publisher	Number of Reviewed Articles	Indexing Database	Number of Reviewed Articles
Springer	20	Scopus	33
Elsevier	32	Directorate of Open Access Journals	17
Taylor & Francis	10	African Journal Online	11
SAGE	8	Web of Science	49
Wiley-Blackwell	6		
PLOS ONE	9		
MDPI	21		
Hindawi	4		
Total reviewed articles	110		110

3. Invasive Plants of Sub-Saharan Africa and Their Deleterious Impacts

There are many IAPs that have been reported in SSA countries [6,70–72]. Table 2 provides examples of detrimental IAPs found in SSA. They are widely distributed throughout the region and have a major impact on the natural environment, biodiversity, and livelihoods [70,72,73]. Numerous IAPs emit secondary compounds, or allelopathic chemicals, which can change the soil chemistry or physicochemical characteristics, including microbial populations, soil organic matter content, and the availability of nutrients [74–77]. For instance, *Acacia mearnsii* and *Acacia melanoxylon* have been reported to increase soil nitrogen levels and alter soil nutrient cycling [74,75]. Increased commodity traffic, the movement of people and tourists from different parts of the world, anthropogenic activities, and climate change led by globalization are responsible for the influx of IAPs and their spread [16,71,74]. SSA has the highest IAP vulnerability among all the countries due to increasing anthropogenic activities and climate change [71].

The widespread alien plant invasion of natural systems in SSA has led to a decline in the biomass of some native species, the disruption of ecosystem services and functions, and the loss of the aesthetic and economic values of ecosystems [70,77]. Also, the spread of IAPs is increasing disease transmission in SSA countries, as some species have been reported to be host disease vectors or pathogens [70,78]. Agha et al. [70] state in their review that certain IAPs can interact directly with the vectors, thereby increasing the risk of certain arbovirus transmission. And Nyasembe et al. [78] found that female malaria vector *Anopheles gambiae* increased fitness and energy reserves when fed on *Parthenium hysterophorus* L., *Ricinus communis* L., and *Bidens pilosa*.

Table 2. IAPs in Sub-Saharan Africa, their native range, and their negative impacts.

Scientific Name	Common Name(s)	Native Range	Impacts	References
<i>Acacia mearnsii</i> De Wild (Family: Fabaceae)	Green wattle, Black wattle, or Late black wattle	South-eastern Australia and Tasmania	Averts native species growth, decreases rangeland productivity and surface water, raises the amount of soil nitrogen, and alters its physicochemical characteristics.	[16,74]
<i>Acacia melanoxylon</i> R. Br (Family: Fabaceae)	Blackwood acacia, or Blackwood	South eastern Australia	Drives away native plant species, and modifies soil nutrients by adding nitrogen.	[16,70,74]
<i>Argemone mexicana</i> L. (Family: Papaveraceae)	Mexican poppy or Mexican prickly poppy	Central America and the Caribbean	Poisonous to livestock; it is rarely eaten, causes health disorders, and exerts allelopathic effects on native plants.	[16,64,70,74]
<i>Bidens pilosa</i> L. (Family: Asteraceae)	Blackjack	Tropical America	Hinders the growth and establishment of native plant species. Also, it competes with crops for resources (water, nutrients, light, and spaces)	[16,74]
<i>Caesalpinia decapetala</i> (Roth) Alston (Family: Fabaceae)	Cat's claw, Mauritius, or Mysore thorn	Asia mainly India	Its impenetrable thickets prevent peoples' and animals' free movement; its massive spines on the stems hinder the management of forests, also harm wildlife, livestock, and people.	[16,74]

Table 2. Cont.

Scientific Name	Common Name(s)	Native Range	Impacts	References
<i>Calotropis procera</i> (Aiton) W.T.Aiton (Family: Apocynaceae)	Sodom apple, king's crown, rubber bush, or rubber tree	South and Western Asia, North Africa, and Tropical Africa	Displaces native plants, grows into dense thickets, and its sap irritates the eyes severely. When consumed, it makes people sick.	[16,74]
<i>Chromolaena odorata</i> (L.) R. M. King & H. Rob. (Family: Asteraceae)	Siam weed, Rouge plant, Christmas bush, or Devil weed	South and North America	Lowers rangelands productivity, suppresses native plants leading homogenization, toxic to animals including human, and intensifies fires.	[16,74]
<i>Clidemia hirta</i> (L.) D. Don (Family: Melastomataceae)	Clidemia, Soapbush, or Koster's curse	Tropical America	Harmful to livestock, suppresses native vegetation, and forms thick or dense stands.	[16,74]
<i>Datura stramonium</i> L. (Family: Solanaceae)	Thorn apple, Jimson weed, devil's trumpet, or devil's weed	Central, South and North America	Forms monospecific dense stands that replace native species, and it is harmful to animals and plants.	[16,70,74]
<i>Lantana camara</i> L. (Family: Verbenaceae)	Lantana	South America and Central America	Lowers the production of fodder, inhibits the growth of vegetation, and destroys or leads to biodiversity loss.	[16,74,76]
<i>Leucaena leucocephala</i> (Lam.) de Wit (Family: Fabaceae)	White leadtree, River tamarind, Pearl wattle, or Jumbay	Southern Mexico and Northern Central America	Displaces native flora and fauna species, changes the ecosystems structure, disrupts primary succession processes, and decreases environmental quality.	[16,74]
<i>Mimosa diplotricha</i> C. Wright ex Sauvalle (Family: Fabaceae)	Giant false sensitive plant or Giant sensitive plant	Tropical America	Produces shadows that stop light-demanding plant species from regenerating; thick stands make it difficult for animals and wildlife to roam freely. Additionally, it poisons animals.	[16,70,74]
<i>Mimosa pigra</i> L. (Family: Fabaceae)	Giant sensitive tree	South America	Decreases native biodiversity, blocks the open habitats used by wildlife, modifies the ecosystem, and reduces native resources and grazing areas for livestock and wildlife.	[16,72,74]
<i>Parthenium hysterophorus</i> L. (Family: Asteraceae)	Carrot weed, or Whitetop weed	North and South America	Toxic invasive plant; it rapidly suppresses native vegetation through allelopathy and resource competition. Alters native plant community structure to monospecific stands, reduces rangeland productivity and crop yields, and causes health problems to people and animals.	[33,50,72,78,79]
<i>Opuntia ficus-indica</i> (L.) Mill. (Family: Cactaceae)	Sweet prickly pear, India fig opuntia, Barbary fig, or Cactus pear	North America	Its spines hinder access to pasture and harm humans, animals, and wildlife, and drives out native species.	[16,74]
<i>Opuntia stricta</i> (Haw.) Haw. (Family: Cactaceae)	Erect prickly pear	Tropical America	Its spines hinder access to pasture and injure people, animals, and wildlife, and displaces native species.	[16,74]
<i>Pinus patula</i> Schiede ex Schltdl. & Cham. (Family: Pinaceae)	Patula pine or Spreading-leaved pine	Central America, e.g., Mexico	Its dense stands displace and/or inhibit the growth and germination of native plants and reduce drainage or water run-off.	[16,74]
<i>Pistia stratiotes</i> L. (Family: Araceae)	Water cabbage, Nile cabbage, Water lettuce, or Shellflower	Probably Tropical America or Africa	Impedes fishing, obstructs waterways, slows down water flow, destroys fish rookeries (breeding colonies), increases nutrient loading and siltation rates (thus, depresses water quality), and threatens fish and other species survival.	[16,74]
<i>Prosopis juliflora</i> (Sw.) DC. (Family: Fabaceae)	Mesquite	Tropical America	Depletes groundwater, lowers ecosystems and rangelands ability to support wildlife, and eradicates native species from invaded areas.	[16,72,74]
<i>Psidium guajava</i> L. (Family: Myrtaceae)	Common guava	Central America and the Caribbean	Makes thick stands that hinder or displaces native species; uses allelopathy to negatively impact plants and crops.	[16,58,74]
<i>Ricinus communis</i> L. (Family: Euphorbiaceae)	Castor bean	East Africa	Forms thick stands that, especially in riparian areas, supplant native plants.	[16,74]
<i>Rubus niveus</i> Thunb. (Family: Rosaceae)	Ceylon raspberry, Mysore raspberry, or hill raspberry	East and South Asia, Australia, or the Himalayas	Transforms the plant community and forms dense thickets that interfere with or impede the growth and rejuvenation of native plants.	[16,72,74]
<i>Senna spectabilis</i> (DC.) H.S. Irwin & Barneby (Family: Fabaceae)	Golden wonder tree	Tropical America	Inhibits the growth and rejuvenation of native plants using allelopathy.	[16,74]

Table 2. Cont.

Scientific Name	Common Name(s)	Native Range	Impacts	References
<i>Tagetes minuta</i> L. (Family: Asteraceae)	Wild marigold	South America	Forms monospecific stands by suppressing the growth and germination of native plant species.	[16,72,74]
<i>Tephrosia vogelli</i> Hook. f. (Family: Fabaceae)	Fish bean or Fish-poison bean	Tropical Africa	Its leaves are toxic to animals including fishes, worms, insects, molluscs, toads, and frogs.	[16,70,74]
<i>Tithonia diversifolia</i> (Hemsl.) A. Gray (Family: Asteraceae)	Mexican sunflower, Tree marigold, or Japanese sunflower	Mexico and Central America	Decreases the productivity of rangelands, modifies the organization of plant communities, and leads to the loss of some native species.	[16,74]

Furthermore, as IAPs' invasions continue to expand in the region, so do the costs of eliminating the IAPs [17]. According to the CBD, IAPs and other invasive species ruin the global economy by billions of dollars every year [16,55]. Thus, because of the IAPs' negative effects on agricultural production [71], biodiversity conservation, human health [70,78], and other socioeconomic development activities in SSA [16,36,77,80], the UN SDGs are in peril. Subject to socioeconomic factors, anthropogenic activities, and climate change [81], IAP invasions are likely to increase further in the future, mainly in arable and urban environments in SSA [72,76]. Therefore, in order to effectively manage IAPs, strategic management plans combining their functional traits and RS should be taken into account. This is because RS can help to detect and utilize high-resolution imagery and functional traits to identify, monitor, and manage IAPs before they spread and cause further negative impact.

4. Implications of IAPs for Sustainable Development Goals in Sub-Saharan Africa

The management and prevention of biological invasions are being widely discussed in a number of international conventions (e.g., CBD, Ramsar Convention, Bern Convention), organizations (e.g., International Union for Conservation of Nature), policies, and initiatives intended to promote sustainable development, biodiversity conservation, human health, and other socioeconomic development challenges [6,16,36]. Therefore, it becomes essential to avert IAPs to ensure a healthy environment that supports sustainable development through biodiversity resources and human health in order to achieve the UN SDGs [36,82]. The UN SDGs and human livelihoods—such as farming and livestock rearing—are supported by healthy, uninvaded ecosystems because they offer ecosystem services such as controlling water flow, foraging, recycling nutrients, producing food—such as seeds, fruits, and vegetables—controlling climate change, and biodiversity conservation [82,83]. However, the invasions of IAPs on pristine ecosystems in SSA could result in the loss of biodiversity and valuable ecosystem services [2,80] with a deleterious impact on human livelihoods (decreases in or losses of crop yields or livestock productivity) and eventually failure to meet the SDGs [72]. In SSA, biological invasions caused by IAPs have proven to be a significant problem toward achieving the UN SDGs [16,36,83]. Some of these SDGs that are directly connected to global biological invasion management efforts to ensure sustainable livelihoods, biodiversity conservation, human health, sanitation, and zero carbon emissions include SDG 1 (ending or eliminating poverty), SDG 2 (zero hunger), SDG 3 (good health and well-being), SDG 6 (clean water and sanitation), SDG 13 (combat climate change), and SDG 15 (life on land).

As IAPs (e.g., *B. pilosa*, *P. hysterophorus*, and *P. stratiotes*) reduce crop yields, it could be difficult for people to achieve food security [78,83]. In developed countries, AIPs are responsible for reducing crop yields by 10% [16]. In Africa, especially in SSA, alien invasive plants alone cause about a 25% decline in yield [16]. In Ethiopia, it was reported that AIP, i.e., *P. hysterophorus*, reduced the yield of finger millet, sorghum, and other vital subsistence crops by 75% [16]. Limited food (and nutrients) could affect other essential livelihoods needed by people, consequently increasing the poverty level and diseases and failing to achieve SDGs 1 and 2 [36]. IAPs can further affect the achievement of SDG 3 because they

pose potential harm to human health because some are toxic to humans and animals e.g., *P. hysterophorus*, *A. Mexicana*, *C. hirta*, *T. vogelli*, and *O. stricta* [74,79]. People's health risks might increase if they are exposed to areas invaded with toxic IAPs.

IAPs (e.g., *P. stratiotes*) can cause pollution in aquatic ecosystems, causing a loss of clean water and aquatic species [70,74,78], which affects the achievement of SDG 6. *Pistia stratiotes*, *Salvinia molesta*, and *Pontederia crassipes* (formerly *Eichhornia crassipes*), for instance, have been reported to increase nutrient loading and siltation rates in lakes and rivers, thereby reducing water quality and subsequently reducing fish survival [16,74]. This could lead to diseases and health problems for people who use such water. Moreover, some IAPs (e.g., *P. juliflora*) tend to deplete groundwater, making water unavailable to humans, plants, and animals. This could make it difficult for humans and animals in SSA countries to have good health and well-being (SDG 6).

The spread and effects of IAPs are not only exacerbated by climate change [81] but they also actively contribute to it. Certain native plants that are effective carbon sinks could be suppressed or undergo major changes in their structure, function, and composition [16]. Additionally, IAPs can alter temperature and precipitation patterns and seasonal distributions in ways that benefit IAPs [16]. Thus, invasive plants impede efforts to mitigate climate change and accomplish UN SDG 13 [36,82]. Furthermore, the invasions of IAPs on the environment can negatively impact land-based life [82]. In SSA, for instance, by damaging the habitats (i.e., changing species composition and structure) that provide vital ecosystem services (food, forages, medicine, water, and nutrient cycling) to sustain humans and nonhuman biota, IAPs threaten the lives of many terrestrial native species with extinction [80]. They may impair humans' and other animals' health because some IAPs influence disease transmission by hosting disease vectors or pathogens, for instance the invasive *Parthenium hysterophorus* [70,78]. The disease might cause the loss of keystones and other vulnerable species, which could lead to an ecosystem imbalance or collapse. Because of this, IAPs impede the effort to protect the lives of species on land (UN SDG 15). In SSA countries, the loss of terrestrial biodiversity due to IAPs could further affect the livelihood and economy of millions of people, impeding the achievement of the UN SDGs [76,77,82]. To achieve UN SDGs in SSA, the planning and management of IAPs are important and could be facilitated through integrating invasive functional traits and RS.

5. IAP Functional Traits and Their Ecological Importance

Despite the fact that an IAP's invasion depends on the recipient ecosystem's resilience, it mostly rests on various functional traits [4,5,17,21], which influence the success or failure of an alien plant in the invaded habitat [18,69]. Functional traits (Table 3) define the ecological strategies that shape plants' responses to different environmental conditions [17,84] and are vital in studying biological invasions as they provide insights into the mechanisms that underlie the plant's biological invasion [4,84,85]. They help to understand why specific plant species may become invasive in their new habitats [69,85,86], determining how IAPs respond to environmental filters, changes, and biotic interactions and how they impact ecological processes [27,87]. For researchers in SSA, this information is crucial since it may aid in planning and developing strategies for managing and controlling IAPs. They might also utilize this information to stop new invasions and restore affected ecosystems. However, as already mentioned, multiple suite of traits are thought to make a species invasive and successful [69,87].

Table 3. Functional trait categories associated with IAPs in Sub-Saharan Africa.

IAP Functional Trait Categories	Ecological Importance	References
Reproduction, spread and growth rate (seed mass, seed number, dispersal method, relative growth rate)	IAPs have a higher fecundity (or reproduction rate). They make significant reproductive investments, resulting in a large number of seeds that can swiftly invade new areas. Their high fecundity makes them compete more successfully than native species.	[4,17–21,34,37,84,87,88]

Table 3. Cont.

IAP Functional Trait Categories	Ecological Importance	References
Reproduction, spread and growth rate (seed mass, seed number, dispersal method, relative growth rate)	IAPs have efficient and different seed dispersal mechanisms. Propagule size, weight, shape, water dispersal (<i>hydrochory</i>), wind dispersal (<i>anemochory</i>), dispersal, animal dispersal (<i>epizoochory</i>) are examples of seed dispersal traits.	[84,87–89]
	As IAPs devote a greater number of resources to growth and reproduction, they grow faster than native species.	[18,37,84,87,90]
Phenology	In contrast to native species, IAPs can alter their phenological patterns. This makes it possible for them to take advantage of resources when there is little competition. IAPs also begin flowering earlier and continue flowering for longer than native plants.	[19,21,66,91,92]
Resource acquisition and utilization (leaf economic spectrum traits)	IAPs' functional traits related to resource (water, nutrients, and light) acquisition include leaf area (LA), specific leaf area (SLA), vein length per unit area (VLA), leaf mass per area (LMA), leaf area, rapid growth rate, height, and extensive and deep root system. These traits indicate IAP's ability to capture and use resources efficiently, which enables them to surpass native species.	[4,17–21,37]
Hydraulic traits (vein traits and drought tolerance traits) and water use	Most IAPs are able to grow in a variety of environmental conditions because they possess traits associated with severe drought and/or temperature resilience or tolerance. For instance, most IAPs show high venation, leaf water potential at turgor loss point, and leaf osmotic potential at full turgor. But some IAPs may have lower drought resistance than natives.	[4,7,19,21,48,93]
Mycorrhizal associations	IAPs' access to nutrients may be influenced by their mycorrhizal associations. Some IAPs may exhibit flexibility in forging associations or have a variety of mycorrhizal partners.	[7,18,93]
Allelopathy and chemical defense	Some IAPs produce secondary metabolites or allelochemicals that inhibit the growth of native plants. They use these allelochemicals to influence their invasiveness and reduce competition with their nearby native species.	[64,72,89]

Other functional traits that have been investigated in various studies include leaf dry matter content (LDMC), leaf nitrogen (LN), potassium (LP), and phosphorus (LPh) content, carbon-to-nitrogen ratio (C:N) [4,9,21,27], leaf area ratio (LAR), leaf area–sapwood area ratio (LA:SA), saturated water content of the wood (SWC), wood density (WD), leaf lifespans (LL), midday leaf water potential (Ψ_{leaf}) [4,37,94], chlorophyll, anthocyanin, leaf orientation, wood specific gravity (WSG), and carotene concentrations [53,60,95]. Previous comparative studies and meta-analyses between IAPs and native species reported that IAPs tend to share functional traits that favor fast growth, giving IAPs an advantage over native species in resource acquisition and utilization [21,90]. Indeed, IAPs typically have higher values of traits related to resource (water, nutrients, space, and light) capture and use compared with native plant species [4,91]. Most of the acquired resources are relocated for reproduction and growth [90,94], which makes the IAPs have a higher fecundity and rapid growth rate than natives [37,84]. Investing in vegetative growth, for instance, promotes population persistence following establishment [92], while allocating enough resources for reproduction encourages invasions of new environments [84]. Furthermore, IAPs tend to have higher plant height, SLA, seed number, and leaf area than native species (Table 2) [19,34]. Indeed, the majority of IAPs are fast-growing (or possess an acquisitive strategy), with higher LL, photosynthetic rates, and nitrogen content [58,92,95,96], while native plants grow slower, since they typically have a more conservative strategy.

It was reported that alien species display a stronger capacity for resource acquisition than native species, which exhibited a resource conservative strategy [4]. They further established evidence that IAPs exhibit higher values of SLA and VLA, which demonstrate lower carbon investment in the construction of a leaf and higher water transport efficiency, respectively. High photosynthetic rates and water transport efficiency are generally due to a higher venation network in IAP leaves [21]. And higher SLA in IAPs implies that they reduce the expense of leaf construction and maintenance [21]. However, native plant species may behave in the exact opposite way; evidently, they invest greater resources into constructing leaves, thus lowering SLA [4,21]. A study carried out on a mountain in central Argentina revealed that native species *Polylepis australis* switched to more conservative resource-use strategies (lower LA, LAR, SLA, and higher LDMC and WD), while an invasive *Cotoneaster franchetii* maintained acquisitive resource-use strategies (i.e., high SLA, LAR, LA,

and low LDMC) along an elevation gradient [37]. A successful water-transport strategy was also demonstrated by *C. franchetii*, which showed low WD and high Ψ_{leaf} and LA:SA [37].

A study conducted by Tordoni et al. [21] using $\delta^{13}\text{C}$ as a functional trait found considerably lower values of $\delta^{13}\text{C}$ in IAPs, suggesting higher gas exchange rates than natives. This result supported the hypothesis that IAPs have a higher rate of photosynthesis [4,21]. On the other hand, IAPs showed a capacity to resist and survive environmental stressors, i.e., drought, extreme temperatures, and/or salinity, because they possess drought and salinity tolerance and environmental plasticity traits [4,69]. Moreover, the phenological traits of some IAPs provide them with the ability to exploit resources differently from native plant species [4]. These patterns enable them to take advantage of resources when there is low competition. The flexibility and ability of IAPs to exploit patchy resources are also indicated by high SLA [34,61,92], which denotes higher photosynthetic capability, higher leaf nutrient levels, and greater turnover of leaves i.e., shorter leaf lifespan [20,66]. In terms of their ability to adapt to different light levels, IAPs exhibit more plasticity than native plant species, which is important for plant growth, development, and survival [15,26,48]. Given the previous results, trait divergence has been suggested to enhance the invasion success of IAPs [21,97,98], but the direction of trait differences is not always consistent. In fact, the invasion process is considered strongly context-dependent, as in some environments, IAPs were found to exhibit similar traits to native species [38,39].

Furthermore, there is a strong correlation between biological invasion and reproductive dispersal traits such as seed production, seed dry mass, and seed dispersal mechanisms [15,26,84,89]. Alien species with long-range dispersal are more successful in invading larger areas [84,89]. This is due to their increased likelihood of arriving in previously uninvaded areas [84]. High-fecundity (i.e., large number of seeds) and easy seed dispersal mechanisms (wind-dispersed and animal-dispersed) are advantageous for invasive species because they allow the seeds to spread quickly and invade vast areas in a brief period of time [54,84]. Many native plant species do not possess these traits and, thus, have poor dispersal abilities and are unlikely to colonize habitats [53,89]. In addition to investing heavily in a large number of seeds to increase the likelihood of invasions, IAPs are effective seed dispersants [26,89]. Nevertheless, in contrast to native plant species, they achieve this by reducing seed mass and size [84]. The growth form and architecture (woody, forbs, shrub, herb, or height) affect how much light they receive and how IAPs compete with natives for resources [15]. In view of this, Mologni et al. [84] observed that growth forms (woody, forbs, and graminoids) and dispersal traits effectively predicted the effective alien invaders in the northern New Zealand islands.

Moreover, some alien plant species rely on mycorrhiza symbioses (or plant–fungal associations) to establish and thrive in the environment [18,93]. In the case of IAPs, they establish strong mutualistic relationships with mycorrhizal fungi in their novel range [7]. The association helps them to establish and enhance their invasiveness in their newly introduced area [7,93]. With this association, IAPs capture essential nutrients more effectively than native nearby plants [7,93]. It also enhances carbohydrate flow and tolerance to harmful heavy metals, salinity, root pathogens, and herbivory for IAPs [7,18,93]. Further, to ensure that they continue their invasiveness, they produce allelochemicals that inhibit native plant germination and growth [19,64]. Many IAPs employ these strategies to suppress and outcompete native plant species, eventually changing the structure of the vegetative community to monospecific stands [88]. Additionally, IAPs display some trade-offs between several functional traits to increase their invasiveness, for instance, by allocating enough resources to growth [4,88]. This means that such IAPs prioritize growth over defense mechanisms, which would enable them to spread invasively [4,21]. Based on the roles and significance of functional traits in plant invasions, this review recommends employing them in research aiming at the management and prediction of new invasions in SSA. Incorporating functional in RS would help to predict which plant species are more likely to become invasive and to evaluate the possible ecological and management challenges associated with the invasion [85].

6. Importance of Functional Trait Remote Sensing-Based Research in Plant Invasions

Studies show that RS is an efficient tool for mapping IAPs in diverse environments [92,99,100]. There are several RS platforms that provide spectral data with higher spatial and spectral resolutions and have the potential to produce estimations of functional traits with higher accuracy [55,92,99]. These include, for instance, unmanned aerial vehicles (UAVs: e.g., aircraft and drones), field spectrometers, and satellites [56,92,99,100]. The use of RS in the study of plant invasions extends beyond invasion science to biological invasion management [92,99,100]. It is employed in plant invasion mapping, prediction, and monitoring, as well as in the supply of ecological information for studies on impacts, mechanisms, dynamics, and drivers (Figure 1). Phenological, morphological, and physiological plant functional traits have proven useful in mapping IAPs [92].

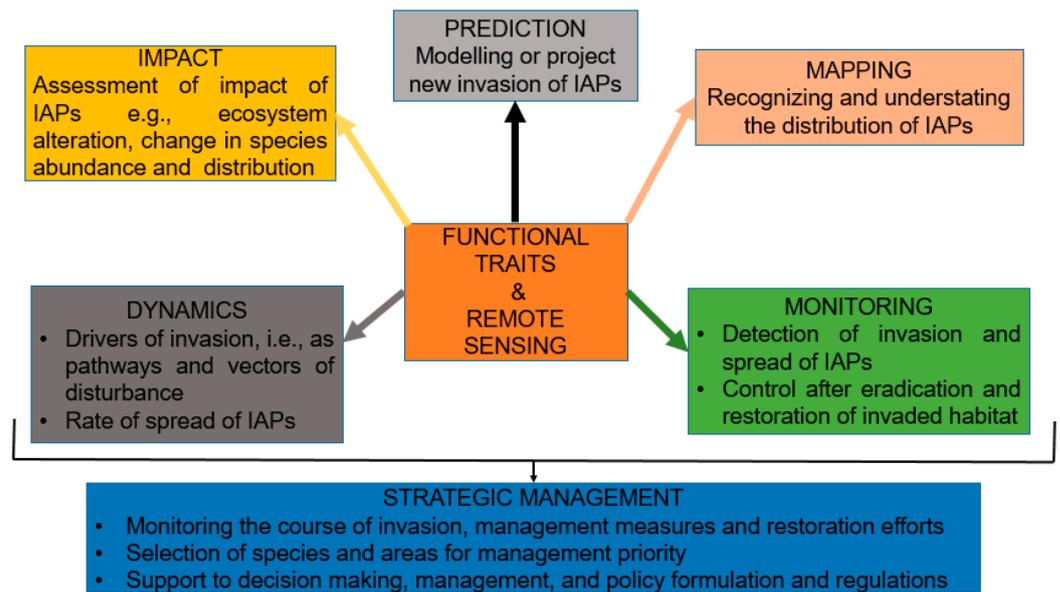


Figure 1. Functional traits and remote sensing's contribution to the knowledge of alien plant invasions and management. Modified from Müllerová et al. [55].

However, its applications for mapping IAPs have often relied on spatial distribution and rarely on functional traits, despite the strong link between IAP invasion and functional traits [4,26,86,101]. Remotely sensed images can be used to detect the physiological, morphological, and chemical qualities of IAPs that correlate to their functional traits [101]. This is due to the fact that variations in spectral band values are also linked to plant biophysical and phenotypic traits [101,102]. Functional traits provide vital information regarding IAPs' success over native species [90,94,103]. Thus, using IAP functional traits in RS (Figure 1) would improve mapping and help predict whether a particular alien plant can become invasive or expand its distribution range [26,92,99]. Given its potential for the mapping and prediction of IAP invasions using function traits, this might be important in SSA, where plant invasions are threatening the UN SDGs and biodiversity conservation [16,36,76,80,83].

Further, the use of an FTRS database can make it possible to continuously and affordably estimate ongoing biological invasions over wide areas in SSA. Such predictions could be useful for extension officers, conservation managers, and farmers in SSA in pre-planning countermeasures for the predicted invasion. Functional traits have been used in RS and various models (i.e., regression and classification trees) to predict the outcomes of alien plant species invasions [56,89,92]. Some studies—the majority of which were conducted in developed countries—have shown how useful it is to study plant invasions using functional traits in RS [61,66–68]. Some of the functional traits of IAPs have been demonstrated, either to aid in mapping and predicting IAPs or to delineate IAPs from noninvasive plant species using RS (Table 4).

Table 4. Functional traits that have been used in RS for mapping and predicting IAPs or to delineate IAPs from noninvasive plants.

Functional Traits	Uses in Remote Sensing	RS Technique	Country	References
Leaves phenology (green or dry leaves)	Monitoring the invasion of <i>Ligustrum lucidum</i> W.T. Aiton.	Satellite	Argentina	[66]
SLA, LDMC, and LNC	Assessing impacts of plant invasions (<i>Impatiens glandulifera</i> Royle and <i>S. gigantea</i>) on ecosystem.	Field spectrometer	Belgium	[61]
Sum of leaf magnesium and calcium contents (leaf Ca + Mg)	Assessing impacts of plant invasions (<i>I. glandulifera</i> and <i>S. gigantea</i>) on ecosystem.	Field spectrometer	Belgium	[61]
LDMC	Verifying statistical models' predictive power using IAPs <i>Festuca rubra</i> L. <i>Elytriagia atherica</i> (Link) Kerguelen, and <i>Puccinellia maritima</i> (Jacq.) Parl.	Satellite	Netherlands	[65]
Flowering periods (flower phenology)	<i>Tamarix</i> spp. invasion detection and mapping using spectral signatures acquired during flowering periods	Satellite	US	[56]
Leaf C:N	Comparing carbon-to-nitrogen ratios of senescent leaf in plants.	Satellite	Bangladesh	[104]
Plant leaf colour (leaf phenology)	Mapping occurrences of IAP <i>Sapium sebiferum</i> (L.) Roxb.	UAV (aircraft)	US	[105]
Patches or clumps (Structural traits)	Mapping of IAP <i>Pennisetum ciliare</i> (L.) Link	Satellite	Mexico	[106]
Total nitrogen, magnesium, canopy height, potassium, and total chlorophyll (Chla + Chlb)	Mapping IAP <i>Lespedeza cuneata</i> (Dum. Cours.) G.Don in grassland ecosystems.	Field spectrometer + UAV (aircraft)	US	[107]
Plant height, inflorescence, flowering, germination, and vegetative growth	Mapping of IAP <i>Spartina alterniflora</i> (Loisel.) P.M.Peterson & Saarela	Field spectrometer	China	[96]
Chlorophyll, anthocyanin, and carotene concentrations	Elucidate functional dissimilarity between IAPs (e.g., <i>Egeria densa</i> Planch., <i>Myriophyllum spicatum</i> L, etc.) and native (e.g., <i>Elodea Canadensis</i> Michx., <i>Stuckenia pectinata</i> (L.) Böerner, etc.).	Field spectrometer + UAV (aircraft)	US	[95]
Canopy structure, senesced leaves, eight, biochemical and biophysical features, and inflorescences	Detecting three different IAP species (<i>Carpobrotus edulis</i> (L.) N.E. Br, <i>Eucalyptus globulus</i> Labill., and <i>Cortaderia jubata</i> (Lem.) Stapf).	UAV (aircraft)	US	[108]
Leaf orientation	Delineating IAP (<i>Taeniatherum caput-medusae</i> L) and native plants.	Field spectrometer	US	[60]
Canopy leaf nitrogen content	Assessing impact of IAP (<i>Morella faya</i> Ait.) invasion on nitrogen-oxide emissions.	UAV (aircraft)	US	[57]
SLA, LMA, water content, carotenoid (Car) content, Chla, Chlb, total chlorophyll (Chla + Chlb), chlorophyll a:b ratio (Chla/Chlb), carotenoid:total chlorophyll ratio (Car/Chl)	Distinguishing IAPs (<i>Hovenia dulcis</i> and <i>P. guajava</i>), from native plant species (<i>Luehea divaricata</i> Mart and <i>Psidium cattleianum</i> Sabine).	Field spectrometer	Brazil	[58]
Canopy, tree diameter, and height	Identification of IAP <i>Acer negundo</i> L in forests.	UAV	Poland	[59]

Previous studies affirm that using optically measured functional traits for remote sensing can help ecologists to better understand the mechanisms and effects of plant invasion (Table 3). Functional traits can be utilized in RS not only to map the invasion of IAPs but also to delineate or group IAPs based on how they share effects on ecosystem processes or how they respond to the environment [54,59,60]. Also, Chacón-Madriral et al. [53] contends that functional traits can be used in RS to determine how closely related IAP species differ in their geographical range sizes. In their study, they used LDMC, SLA, plant height, leaf thickness, WSG, LN, LP, and leaf N:P ratio to determine the geographical range size difference among related plant species. In addition, current studies reveal that plant functional diversity patterns can be detected from the spectral diversity of high-resolution multispectral imagery without the need for satellite data [109,110]. This is because recent developments in algorithms have shown the potential of calculating spectral diversity as a proxy for functional diversity compared with FTRS, which still needs the testing of empirical or theoretical models using data from satellites [109,110]. This could help in highlighting the effects of IAP on an ecosystem scale. Overall, these studies clearly show the relevance of the FTRS research approach to understanding invasive plant behavior and management. Despite the fact that studies that demonstrate the use of FTRS to monitor, predict, and control IAPs are missing or limited in SSA, the functional traits and RS techniques in Table 3 can also be used to study biological invasions of various IAPs in SSA.

Despite the fact that FTRS-based research can be used to detect and predict IAPs and their distribution, it should be understood, however, that without an initial field recognition of the range of a given IAP, remote technology cannot help in monitoring that species. The recognition of species' detailed characteristics (mainly colour and growth forms) in the field can be the key to species determination.

7. Lessons Learned and Way Forward

The alternative way of delineating IAPs from native plants is by using functional traits, as explained by Mallmann et al. [58] and Mielczarek et al. [59]. For instance, in contrast to native plant species, the IAPs tend to have bigger leaves, higher specific leaf areas, minimal defense investments, higher plant heights, and high resource acquisition. Nevertheless, it is important to note that the success of alien species could depend either on a more acquisitive or a more conservative strategy with respect to native species, according to the invasion context. This review underlines further that the utilization of FTRS-based data would advance IAP knowledge and aid in planning and preventing plant invasions in SSA. Even with RS's increased capacity for the assessment of IAPs' functional traits, ecologists in the SSA have failed to keep up with the recent growth in remote-sensing technologies, which has hindered the region from fully utilizing these tools for invasive species mapping, mitigation, and prediction. Given the complexity of mapping invasive species in SSA due to its high diversity of species and structural heterogeneity, the integration of functional traits into RS mapping might be particularly helpful, where IAP species pose a far more serious problem [16,36,58,73,74,76,80]. Hence, the efficiency of biological invasion control may be achieved with better knowledge of invasion dynamics and the identification of their drivers through a FTRS-research approach. In this light, we propose the following objectives to promote the use of functional traits and remote sensing techniques to monitor and contrast IAPs also spread in the SSA region. The first is to promote the use of satellite-derived RS data to study IAP invasion in the SSA region, since a great number of satellite missions (such as LANDSAT and COPERNICUS missions) offer free data that can be easily used by researchers in SSA. Indeed, UAVs and field spectrometer instruments are not cheap, and it might not be easy to use them in countries in SSA. Satellite data (such as LANDSAT and SENTINEL), however, could be analyzed both with medium–high level workstations or under cloud computing frameworks, such as the Google Earth Engine, the usage of which only requires an internet connection and an entry-level laptop. Secondly, there is a need for collaborations between invasion ecologists from developed countries and those from SSA in research-related functional traits and RS to impart FTRS knowledge to researchers in SSA. Furthermore, we recommend that ecologists in the SSA start employing a process-based mapping and biological invasion prediction tool. In doing so, it is expected that the FTRS approach will effectively prevent plant invasions in SSA, improve biodiversity and conservation, and consequently achieve the UN SDGs. However, even though IAPs may share specific functional traits that can be leveraged to improve their detection remotely, it should be noted that the success of detection may vary depending on the species.

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