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Does scale matter for Lantana camara invasion in the Indian floodplains: A perspective

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Abstract

Invasion is a renowned threat to global biodiversity, the process being triggered and facilitated by species-specific as well as site-specific characteristics. Floodplains are ecologically unique ecosystems which are also dynamic in nature. Invasion dynamics across these ecosystems does not only follows a different approach but are highly variable in terms of species establishment and spread. Literature suggests that two schools of thoughts can be derived for these riverine habitats regarding invasion; first, that periodic flooding and inundation limits the growth of invasive plants and second, that it may even facilitate habitat susceptibility to invasion. Taking the case study of the tropical invader *Lantana camara* along with some other major invaders of the Indian floodplains we try to assess the vulnerability of such habitats to these species and infer how site characteristics influence invasion at a local as well as at regional scale.

Keywords: invasive plants, *Lantana camara*, floodplains, site characteristics, habitat modification

Introduction

According to the Convention on Biological Diversity, 'Invasive alien species (IAS) are species whose introduction and/or spread outside their natural distribution ranges threatens the biological diversity'. In the recent times, climate change, changing land-use patterns and various other disturbance regimes have further escalated the problem of invasive species (Kohli *et al.*, 2012) ^[51]. These species not only interfere with the normal functioning of the ecosystem processes but also have negative implications on the ecological as well economic front (Senator and Rozenberg, 2017; Walsh *et al.*, 2016) ^[54, 27]. But not all invasive species are known to dominate across every bioclimatic zone (Chitale *et al.*, 2009) ^[60] possibly because the success of any invasive species in a novel environment is governed by a multitude of environmental, physiological and resistance factors.

Plant invasions, threatening the global ecosystems (Early et al, 2016), are in general mediated by three major factors responsible for their success, viz. 'invasiveness', i.e. the trait values of an invasive species which can be considered a manifestation of its performance ability in introduced ranges (Goyal et al., 2018) [39], 'invasibility' (Davis et al., 2000; Catford et al., 2011) [36, 22] i.e. the vulnerability of the habitat to invasion, and finally on the 'history of species introduction' into a novel range (Vardien et al., 2012) [61]. While studies have focussed on understanding species traits favouring invasion or the role of propagule pressure in promoting invader's success, understanding of species-specific invasibility is still not well represented. Ecosystem vulnerability has been stated as a major factor shaping invasional success. Degree of habitat openness, intensity of disturbance and propagule pressures are important determinants of invasion (Alston & Richardson, 2006) [28]. Empty niches and disturbed habitats are more prone to invasion (Vardien et al., 2012, Hiremath, 2018) [61, 4] with the degree of invasion also being closely linked to the degree of human disturbance (Gao et al., 2018) [29]. Disturbance induced changes in the community act as

invasion windows reducing limiting factors to their growth (Duggin & Gentle, 1998, Alston & Richardson, 2006) [23, 28] and promoting spatial heterogeneity as well as community susceptibility to invasion (Totland *et al.*, 2005). Thus, it can be inferred that the type and intensity of disturbance regime is a strong determinant of the success of any invasive species along with its attributes (Duggin & Gentle, 1998) [23].

Floodplain ecosystems can be viewed as shifting mosaics of plant communities and ecosystem properties (Jager et al., 2019). Characterised by frequent flooding, regular sediment load, nutrient rich woods & meadows, these factors shape the vegetation structure and functionality of the floodplains (Jager et al., 2019; Rawat & Adhikari, 2015). Studying invasive plant presence in the floodplains provides opportunity for us to understand these dynamic ecosystems which not only represent changing site characteristics but also extensive human dominated land-use. Two schools of thoughts regarding invasion can be derived for these ecosystems in the larger context. First, that perennially flowing water may limit establishment of alien plan species in riverine habitats (Alston & Richardson, 2006) [28]. Second, that floods are known to induce disturbance, increase nutrient availability and floodwater may act as dispersing agent for propagule transfer, thus facilitating invasion (Hofle et al., 2014; McShane et al., 2015) [46, 52]. Since relevant studies in this context are lacking, especially for the Indian subcontinent, a quick review of studies pertaining to these ecosystems across the world has been carried out. Our study aims at understanding floodplain susceptibility to invasion by alien species in general and with special reference to the infamous weed, Lantana camara, while also deriving relevant inferences for further management of the species in India.

Floodplain dynamics and invasion

Floodplains are dynamic systems subjected to frequent sediment flux and water flow that exhibit gradients in sediment texture and moisture over space, these properties structuring and shaping the floodplain structure and the ecological communities associated with them (Whited et al., 2007) [10]. Topographic attributes of the floodplain as well as the hydrological regime or flow (Capon, 2003) [56] are both important criteria for determining tropical and temperate floodplain plant communities (Toogood et al., 2007) [55]. Influenced by fluvial processes such as flooding and sedimentation, these ecosystems represent distinctive floristic richness (Andersen, 2003) [16] as compared to terrestrial vegetation and are also regarded as one of the most biologically diverse ecosystems of the world (Richardson et al., 2007; Whited et al., 2007) [12, 10]. Given the above, flood tolerance still remains one of the key determinants of vegetation in such areas, hence a variety of species with a wide range of tolerance to flood are known to establish and coexist in these systems (Hale et al., 2008). The role of environmental factors such as hydrological, geomorphological and disturbance regime (Richardson et al., 2007) [12] in shaping species composition also takes into consideration their competitive & dispersive abilities and the theoretical niche as defined by the species (Toogood *et al.*, 2007) [55]. While duration and depth of inundation is known to influence the distribution of plant species across a floodplain, the adaptations of plants to floodplain environments are not very well known (Finlayson, 2005) [9].

Plant invasiveness is a function of its key traits, namely, physiology, biomass, size, growth rate, fitness, as well as its phenotypic plasticity (Chen et al., 2013) [62]. At the landscape level climatic suitability plays a major role in the spread and establishment of invasive species, whereas at the micro scale nonclimatic factors such as changes in land-use, disturbance, competition and proximity to source areas are known to determine their success (Nath et al., 2019) [1]. Invasive plants can readily establish at sites where soils are naturally bare, e.g. riverbanks, mudflats, or rendered bare by disturbances such as sedimentation, erosion (Zedler and Kercher, 2004; Repka et al., 2015) [24, 47]. River ecosystems are known to be susceptible to alien plant invasions (Repka et al., 2015) [47] due to their dynamic hydrology patterns and the fact that hydrochory (Thomas et al., 2006) [26] acts as a medium for propagule dispersion (Richardson et al., 2007; Foxcroft et al., 2008) [12, 30]. Flooding may cause damage to the existing vegetation creating functional or canopy gaps (Zedler & Kercher, 2004; Foxcroft et al., 2008) [24, 30] and the newly deposited sediments can lead to the formation of new grounds for colonization of opportunist plants with increased resource availability (Zedler & Kercher, 2004; Richardson et al., 2007) [24, 12]. According to the immediate disturbance hypothesis, frequent or continued disturbance factors can lead to replacement of primary species (Anitha et al., 2008) by habitat generalists which can easily adapt to disturbance (Marvier et al., 2004) [24]. Since most invasive species are early seral species taking advantage of disturbance and growing in environments with less competition, such habitats responding positively to disturbance may act as focal points of subsequent invasion to adjacent landscapes (Richardson et al., 2007; Cuda et al., 2017) [12].

Greater tolerance to stress (Chen *et al.*, 2013) ^[62], specialised adaptive morphological structures (Repka *et al.*, 2015) ^[47] and flooding mediated disturbances are believed to give invasive

plants competitive advantage over natives and thus promote the invasion rates substantially under these circumstances (Zedler and Kercher, 2004) [24] and this has been corroborated by several studies all across. In order to predict the impact of flooding on exotic invasive species and natives in a study conducted by Osunkoya et al., 2014 [43] in Australia, it was observed that both the groups of plants had a similar response to disturbance caused by flooding. But the resilience of the exotics was much higher as compared to natives, which might explain their dominance over longer times (Osunkoya et al., 2014) [43]. Hofle et al., 2014 [46] observed that the riparian floodplain forests of Europe were characterised by high degree of invasive woody as well as herbaceous plants, their distribution being influenced by either their stand age, floodplain forest type or by the distance to the nearest waterbody. Hashim et al., 2010 [41] stated that non-native species constituted almost one-fourth of the total species in the floodplain secondary forests of peninsular Malaysia, including invasive like Lantana and Chromolaena. However, it was also noticed that the study area was subjected to anthropogenic pressures in the form of long history of cultivation and settlement, thus providing ample time for the invaders to flourish. The aggressive spread and colonization of the invasive Melilotus alba along the floodplains of Matanuska River in Alaska is supposedly facilitated by upstream roads, mines and agricultural developmental networks (Wurtz et al., 2006) [59]. Rapid invasion of wet prairies by Phalaris arundinacea coincides with the increase in both resource supply and anthropogenic disturbances (Kercher et al., 2006) [58]. Alien species invasion along the Thaya river and the Morava river corridor in Europe can be attributed to higher availability of unused resources because of nutrient fluctuations due to historic flooding and other disturbances (Repka et al., 2015) [47]. Invasion by non-native species was also perceived to be facilitated by flooding in Jefferson National Park, Virginia, while the same being negatively affected by greater resident species richness (Holle and Simberloff, 2005) [7]. Copious seed dispersal and nutrient enrichment promoted by flooding has caused Impatiens glandulifera to extensively spread along the riverbanks in central Europe (Cuda et al., 2017) [20]. Longevity of propagules and their downstream dispersal has also formed grounds for the invasion of Dioscorea oppositeifolia along the stream corridors and floodplains of Illinois (Thomas et al., 2006) [26].

On the contrary, in a study undertaken by Catford *et al.*, 2011 [22] across several riparian wetlands of Australia, it was deduced that most invasive species were not adapted to riparian sites and were unable to withstand flooding. Minimal inundation allowed for their successful establishment. Spartina densiflora, an important invader of the estuarine areas of Iberian Peninsula was also observed to respond negatively to flooding conditions (Mateos-Naranjo et al., 2007) [14]. Its growth and photochemistry efficiency decreased considerably with extended periods of flooding. In a study undertaken by Vivian et al., 2014 [31] to investigate the role of environmental flows in managing the Australian floodplain invasive plant *Juncus ingens*, it was found that regulated environmental flow can be used as a potential tool for controlling its spread, given the fact that its seeds were sensitive to prolonged submergence in water and flooding provided unfavourable conditions for its persistence.

Evidently, for any species to withstand and flourish under flooded conditions it is important for it to inherently have or evolve sustenance measures. Flood adapted species with certain morphological adaptations helps them exploit resources and withstand such frequent and intense disturbances (Richardson *et al.*, 2007) [12]. Morphological adaptations such as reduced belowground biomass, increased shoot lengths (as observed by Miller and Zedler, 2003 for *Phalaris arundinacea*) [48] are some responses of invasive plants to flooding. In a controlled comparative study between an invasive and native species of the genus *Alternanthera* in China it was found that the invasive species *A. philoxeroides* was more tolerant to waterlogging showing lesser sensitivity to growth traits than its native counterpart *A. sessilis* (Chen *et al.*, 2013) [62]. When subjected to artificial flooding condition 100% survival rates of the plant were achieved by means of shoot elongation in order to restore connection between leaves and above surface air (Fan *et al.*,

2014). Varied responses of plant growth in response to changes in soil moisture has also been a determining factor to predict habitat vulnerability to invasion at the microscale level (Nath *et al.*, 2019; Yue *et al.*, 2019)^[1, 35]. In a random investigation of the invasive plant *Mikania micrantha* across the agricultural fields of Pearl River Delta, China, it was deduced that its growth was limited under dry drought like conditions and that wet and inundated conditions stimulated its growth (Yue *et al.*, 2019)^[35]. In a similar investigation by Nath *et al.*, 2019^[1] in the floodplains of Manas National Park, it was observed that *Mikania* was able to sustain full soil water regime whereas another major invasive of the landscape, *Chromolaena odorata*, could proliferate in moderate as the plant requires high light intensity to germinate and prolonged exposure to floods may lead to decrease in seedling emergence.

Table 1: Dominant invasive plant species of the Indian Floodplains along with their invasive characters

Invasive plant	Invasiveness (inherent characteristics)					
•	 Grows well in high nutrient and high light areas, proximity to disturbance sites & corridors, 					
Lantana camara	 Grows in rich as well poor soils including laterite and gravel 					
	 High seed production, easy dispersion 					
	 Aggressive colonizer of moist habitats 					
Mikania micrantha	 Grows in most soil types-acidic or alkaline, fertile or infertile 					
	 Growth exacerbated by disturbances, colonises wet places, forest clearings and edges very quickly 					
Chromolaena odorata	 Plant of open well drained soils, drier areas. 					
Chromotaena oaorata	 Forest degradation causes quick colonization as seeds require high light intensity to germinate 					
Eichhornia crassipes	ssipes Prevalent in lowland lakes, can cause siltation of wetlands					
Mimosa spp.	 Weed of humid tropical regions 					
mimosa spp.	 Grows best on fertile soils, but can thrive on wide range of soil conditions 					
	 High reproductive capacity and high environmental adaptability 					
Ageratum conyzoides	 Annual weed of arable land, can grow in various habitats 					
Ageraiam conyzoides	 Prefers sandy soils with good moisture 					
	 Produces enormous seeds which are easily dispersed 					
	 Adapted to wide range of habitats, xeric to aquatic 					
<i>Ipomoea</i> spp.	 Easy propagation via vegetative means 					
	 Can grow on dry soils as well as wetlands (across land-water interface) 					
Parthenium hysterophorus	• Weed of wasteland. Grows well on bare, open, disturbed, intensely loaded lands. Copious seed production.					
	 High temperature favourable for growth, prefers alkaline clay, loam soil to heavy black clay soil. Capable of 					
	tolerating water stress					
	 Seed germination requires high soil moisture but the plant can withstand wide range of temperature, moisture, 					
	pH conditions					

Table 2: Occupancy of dominant Invasive flora and causes of habitat vulnerability to invasion across Protected Areas of the Gangetic-Brahmaputra floodplains

Floodplain	Protected Area	Dominant invasive species recorded	Habitat occupied	Invasibility (site characteristic)	Local or regional presence?	Reference(s)
Gangetic floodplain	Dudhwa National Park	Lantana camara	Roadsides, forest edges, excessively grazed areas	Low-lying areas prone to flooding during monsoons Rapid urbanisation and land-use changes high biotic pressures	Local	Pers obs; Mathur & Midha, 2008; FSI, 2014; August-Schmidt et al., 2015; Negi et al.,2019
		Parthenium hysterophorus	Highly grazed areas and village peripheries	4) recent alluvial formation of the Gangetic Plain showing a succession of sand and loam beds	-	FSI, 2014
	Valmiki Tiger Reserve	Mikania micrantha	Open moist grasslands along streams	1) Major soil types- bangar hard clay soil, lateritic soil, sandy soil, kankar and saline soil, alluvial soil. 2) human and livestock pressure 3) seasonal inundation	Regional	Chandran, 2015, Maurya & Borah 2013; FSI, 2014; Nath <i>et al.</i> , 2019; DNPWC, 2016; Zhang <i>et al.</i> , 2004
		Phoenix humilis	Open hill forests		-	
		Chromolaena spp.	Blanks along roads		-	
						Singh & Khare, 2020

	Pilibhit Tiger	Lantana camara	_		_	
	Reserve	Ageratum conyzoides	-	1) Rapid urbanisation and	<u>-</u>	Singh & Khare, 2020
		Parthenium		land-use changes		
		hysterophorus	-	2) High biotic pressure	-	Singh & Khare, 2020
		Ipomoea carnea	-		-	Singh & Khare, 2020
	Chitwan National Park (Nepal)	Lantana camara	Wetland, riverine forest, sub-tropical mixed forest, short grassland, tall grassland and sal forest	1) Riverine, subtropical vegetation 2) Disturbance prone with high biotic pressure and landuse changes	-	Murphy et.al., 2013; DNPWC, 2016; August-Schmidt et al., 2015; Zhang et al., 2004; Negi et al., 2019; Thapa et al., 2014
		Mikania micrantha	Closer to main rivers, and riverine hardwood forests, wetter zones		Regional	
		Chromolaena odorata	Wetland, riverine forest, short grassland, sal forest, sub- tropical mixed forest and tall grassland, drier zones		-	
	Shuklaphanta Wildlife	Lantana camara	Grasslands and outskirts of the forest	-	-	Bhattarai, 2012; August-Schmidt <i>et al.</i> ,
	Reserve (Nepal)	Eichhornia crassipes	-		-	2015; Negi et al., 2019
	Kaziranga Tiger Reserve	Lantana camara	Forest edges, buffer, degraded lands	1) Rich alluvial soil 2) disturbance in the form of annual flooding & erosion 3) park encroachment due to growing human population	Local	Pers obs; Lahkar et al., 2011; Hiremath & Sundaram, 2013,; Nath et al., 2019; DNPWC, 2016; August-Schmidt et al., 2015; Zhang et al., 2004; Negi et al., 2019
		Mikania micrantha	Almost every habitat type		Regional	
		Mimosa diplotricha	Grasslands, woodland, western ranges		Regional	
	Orang National Park	Mikania micrantha	Grasslands	alluvial floodplain surrounded by human habitations on the periphery	Regional	Lahkar <i>et al.</i> , 2011;
		Mimosa diplotricha	Along the river, especially in the western areas		-	Hiremath & Sundaram, 2013; Choudhury <i>et al.</i> , 2017; Nath <i>et al.</i> , 2019; DNPWC, 2016; Zhang
		Chromolaena odorata	-		Regional	<i>et al.</i> , 2004; Kohli <i>et</i>
		Ageratum conyzoides	-		-	al., 2006
Brahmaputra	Pabitora Wildlife Sanctuary	Ipomoea spp.	Grasslands	1) Flat floodplain and tropical	Regional	Lahkar <i>et al.</i> , 2011; Hiremath & Sundaram,
floodplain		Mikania micrantha	-	evergreen forest. Clayey soil	-	2013; Royal & Goyal, 2014; DNPWC, 2016; Nath <i>et al.</i> , 2019; Lalita & Kumar, 2018; Zhang <i>et al.</i> , 2004
		Parthenium hyetrophorus	-	with silt content 2) Livestock grazing erosion	-	
	Manas National Park	Chromolaena odorata	Grasslands, southern boundary of the park	1)Low-lying flat areas prone to inundation, northern part composed of limestone and sandstone is of savanna type, southern grasslands comprise of fine alluvium	-	Lahkar <i>et al.</i> , 2011, Royal & Goyal, 2014; Nath <i>et al.</i> , 2019;
		Mikania micrantha	Grasslands, riverine patches, forest edges		-	DNPWC, 2016; Zhang et al., 2004
	Garumara Wildlife Sanctuary	Mikania micrantha	-	-	-	Hiremath & Sundaram, 2013; Lahkar <i>et al.</i> , 2011; DNPWC, 2016; Zhang <i>et al.</i> , 2004

		Chromolaena odorata	-		-	Hiremath & Sundaram, 2013; Lahkar <i>et al.</i> , 2011; Nath <i>et al.</i> , 2019
	Jaldapara Wildlife Sanctuary	Mikania micrantha	Grasslands, especially with primary woodland succession	-	-	Hiremath & Sundaram, 2013; Lahkar et al., 2011; DNPWC, 2016; Nath et al., 2019; Zhang et al., 2004
	Laokhowa Wildlife Sanctuary	Mikania micrantha	-		-	_
		Mimosa spp.	-	-	-	Nath, 2013; Nath <i>et al.</i> , 2019; DNPWC, 2016;
		Chromolaena odorata	-		-	Zhang et al., 2004
		Eichhornia crassipes	-			
	Dibru-Saikhowa National Park	Lantana camara	-	Villages within the core area, subject to human disturbance and resource dependency, tropical monsoon climate	-	Purkayastha et al., 2005;Das et al., 2005

Role of site characteristics and scale of invasion: Current scenario for invasive species of the Indian floodplains

The Gangetic floodplains and the Brahmaputra floodplains, have, since ages been the centre of agriculture and human settlements in India. Anthropogenic disturbances and associated dramatic changes in land form are not new for these catchments. Protected areas in both these floodplains are dominated by woodland vegetation and grasslands that serve as major habitats for large herbivores like the One-Horned Rhinoceros, Wild Buffalo and the Asiatic Elephant and certain specialists like the Swamp Deer. Lantana camara, classified as one of the top ten worst invaders of the world (Carrión-Tacuri et al., 2011) [19] has widely naturalised across several countries (Pandey & Chauhan, 2012) [17], including India. Here it has almost colonised every habitat and landscape type at varying scales and distribution intensities, ranging from the tropical evergreen forests of Southern India, to tropical and subtropical moist and dry deciduous forests of the Himalayas, Western Ghats and Central India (Hiremath and Sundaram, 2013) [3]. Predicted climatic suitability in these major biodiversity hotspots is likely to promote range expansion in the coming years for several invasive species including Lantana (Lamla et al., 2018) [45]. However, for now it is known that Lantana is unable to withstand frost and proliferate under dense, intact canopies, and avoids saline, boggy or hydrophobic soils (Pandey & Chauhan, 2012) [17], which most of the Terai and floodplain habitats are characterised by. Compared to the Western Ghats and Deccan Peninsular biogeographic zones, this invasive plant shows negligible presence in these floodplains. And although its presence is sporadic as of now, the landscape is still increasingly becoming susceptible to its growth, while also being invaded by other serious invaders. Thus, in order to understand the vulnerability of floodplain habitats to IAPs, a review regarding invasion mediating factors for the dominant invasive plants of these regions was carried out (Appendix-I).

Conclusion and way forward

Plant communities in a floodplain or riparian area are organised and differentiated based on the environmental niche of individual community members along a gradient of wet to dry (Garssen *et al.*, 2015). In general, wetter zone communities, which are more susceptible to flooding processes such as germination, are distinctively different to dryer zone communities, which are

associated with drying related processes such as competition, mortality (Capon, 2003) [56]. Distribution of native as well as nonnative plants in these ecosystems are strongly correlated to climate, hydro-geomorphology and their history of introduction (McShane et al., 2015) [52]. Environmental variables such as hydrology and temperature correspond more strongly to native species than the invasives which relate more to site related variables (Flanagan et al., 2015) [40]. Thus, response of these vegetation communities to hydrological regime is speciesspecific and highly dependent on flooding intensity, with a number of species able to withstand flooding conditions (Garssen et al., 2015)^[2]. In order to make such predictions on the response of plant communities to flooding events and furthermore on the susceptibility of floodplain ecosystems to invasion requires long term research and monitoring (Toogood et al., 2007) [55]. While species traits are known to confer invasiveness, habitat characteristics and disturbance types influencing invader-native community interactions, are also critical to determine their success (Lake and Leishman, 2004) [25], Key functional traits of plants deterministic of their establishment and spread in their invaded ranges, but this too depends on the environmental context and spatial scale taken into consideration (Goyal et al., 2018) [39]. Disturbance often leads to promoting invasion at the local scale (Vardien et al, 2012) [61].

Unlike the temperate Himalayan vegetation, tropical, sub-tropical deciduous forests of the Indian subcontinent where Lantana has largely invaded, its invasion in the Protected area of Indian Gangetic and Indian Brahmaputra floodplains is still in its genesis, reported in its least form. The site characteristic of any 'region' of this landscape is the same throughout, high moisture content and salinity along with high water erosion and disturbance factors. Thus, flooding regime alone cannot account for its absence or patchy distribution; habitat type, soil properties, and other disturbance regimes are expected to play an important role determining its distribution across these landscapes. These ecosystems being fertile and productive are more prone to human interventions and disturbance. Significant landuse-landcover changes induced by these external pressures are potent to bring about changes in site characteristics initially at a smaller scale, making them as the driving factors for localised *Lantana* invasion along the disturbance sources. Projecting the current pace of rampant habitat destruction and anthropogenic changes, there is

a high probability of inviting the spread of its invasion to the entire habitat as well. From the above theories and discussion, we can infer strongly that despite of floodplain ecosystems not being completely conducive to the growth of the invasive plant Lantana camara on a regional scale, the site characteristics can play a vital role in its establishment at a local scale. And since our current understanding on different aspects of invasion by Lantana is hindered by the fact that it exists as a species complex with high phenotypic plasticity (Goyal et al., 2018) [39], a more conclusive study is thus required in the context of presence of Lantana in these floodplains and the probable factors that have favoured the process of successful invasion in a local vs. regional dimension. Another major gap highlighted by this review would be to undertake extensive studies covering the above facets of invasion which not only are site-specific but also encompass comparative case studies from other landscapes as well for the Indian subcontinent wherein species-specific response to flooding, inundation, and other associated disturbance types can be documented for carrying out a comparative analysis between native and invasive species.

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