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Research Article
Clonal Growth Strategies and Their Impact on Plant Invasiveness in the Aquatic Ecosystems of the Kashmir Himalaya

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Abstract

Background and Objective: Despite its significance in invasion biology, the study of functional traits driving plant invasiveness has been somewhat underexplored. Clonal growth, however, is recognized as a key trait that enhances spatial expansion and regeneration in invasive plants. It is aimed to document the clonal growth organ spectra in alien aquatic plant species and to understand clonal growth organs role in aquatic plant invasiveness. **Materials and Methods:** Macrophytic species were broadly categorized based on clonal architecture, space occupancy strategies, life form and nativity. To capture plant diversity across littoral to limnetic zones, multiple transects were set, with 30 quadrats of varying sizes (0.25-5 m^2) along each transect to assess diversity and abundance. Invasion stages were determined using the spatial spread model (CM model). Spearman's rank correlation and K-mean cluster analysis were carried out to assess the statistical significance. **Results:** The results demonstrated significant differences in the distribution pattern of clonal and non-clonal alien plant species. Out of 88 target alien species, 83 species were found to be clonal and all the clonal species were found to be highly invasive and predominantly use guerrilla strategy of space occupancy. The data showed a significant positive correlation ($p<0.05$) between clonality and invasiveness. Eutrophication seemed to favor species with a guerrilla strategy mainly. **Conclusion:** The study concluded that clonality in aquatic ecosystems has a significant influence on species invasiveness. In an evolutionary context, differences in clonal architecture might represent differences in the foraging strategies of clonal plants, which in turn has useful management implications for invasive species.

Key words: Clonality, invasive species, clonal growth organs, biological invasion, aquatic ecosystems

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Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Biological invasions and ensuing homogenization of the world's biota seriously threaten native biodiversity and are increasingly viewed as critical forms of global environmental change[1]. A recent cross-continental study revealed that invasive plants drastically reduce native plant diversity in non-native habitats while causing minimal impact in their native ranges[2]. Disturbance is ubiquitous not only in terrestrial ecosystems but also in aquatic ones[3,4]. Aquatic habitats, especially lakes and wetlands, being resource-rich are highly vulnerable to invasion[5,6]. Even though $\leq$6% of the Earth's land mass is wetland, 24% (8 of 33) of the world's most invasive plants are wetland species[5]. Moreover, many aquatic plants are characteristically invasive due to the immense potential of rapidly increasing their spatial distribution[7]. Concern over the ecological and economic impacts of biological invasions has generated tremendous interest in the factors controlling invasion success[8,9]. Numerous studies have examined the traits of successful invaders[10,11] and the types of communities most susceptible to invasion[12,13]. Other studies have linked broad native range and mutualistic facilitation to invasive success[2,14]. It is widely accepted that invader attributes, community characteristics and environmental conditions together determine whether or not an exotic plant species can invade a new habitat[15]. However, very few studies have tested traits that help invaders establish in multiple communities under different growing conditions[16,17].

Clonality is a set of attributes that enables a plant to produce genetically identical offspring with the potential to become independent of the mother organism[18]. Modes of clonal growth are diverse as the clonal spread and multiplication are realized through the production of specialized organs of root, stem or even leaf origin. These organs of clonal growth presumably differ in the distance they can spread, in the period for which clonal offspring are connected, in several clonal offspring produced and in other functional traits[19,20]. Studies have shown that clonal growth is more prevalent in environments that are cold, shaded, wet and nutrient-poor, while it is less common in dry and disturbed conditions[21]. The proportion of clonally growing species in wetlands and other aquatic habitats is large and in most aquatic taxa vegetative propagation predominates over sexual reproduction[22,23]. Invaders that reproduce vegetatively (clonal species) generally have a greater ecological impact on native communities than non-clonal species[24] but the relationship between a clonal species' ability to establish and expand is rarely explored. Once established, some clonal species can persist and spread into conditions that are more stressful than those where they colonized[25]. It is very likely that functional traits of species, such as the ones related to physiology, biomass allocation, growth rate, size and fitness, promote invasiveness[26,27], but progress in the search for traits conferring invasiveness has been slow.

The Kashmir Himalaya, part of the Himalayan Biodiversity Hotspot, is home to diverse aquatic habitats that support a wide array of plant species that are native to the geographical landscape. However, despite its location in a mega-biodiverse region, the aquatic ecosystems are highly susceptible to invasions by alien plants[28] and efforts to identify the specific traits that drive these invasions and affect species functionality remain limited. Recently, many lakes and wetlands in this region have been significantly affected by invasive plants, with clonality believed to be a significant factor in their success[29]. Based on preliminary findings, this study aimed to document clonal growth organ spectra in aquatic alien plants of Kashmir Himalaya and investigate whether clonality, as a functional trait, influences their invasiveness and colonization potential. Furthermore, the study explores the relationship between clonal growth organs, invasion success and the trophic status of aquatic systems. Ultimately, this research seeks to understand how clonal growth organs support plant invasions, link these traits to aquatic trophic conditions and provide critical insights to predict and manage invasive risks in similarly resource-rich and pristine ecosystems.

MATERIALS AND METHODS

Study area: The Valley of Kashmir is situated on the Northern Fringe of the Indian Sub-Continent between 33°25'-34°50'N Latitude and 74°-75°0.5'E Longitude covering an area of about 16,000 km^2. Topographically, it is a deep elliptical bowl-shaped valley, bounded by lofty mountains of the Pir Panjal in the South and Southwest and of the Greater Himalaya in the Southeast to Northwest, with 64% of the total area being mountainous. The altitude of the floor of the valley at Srinagar is about 1600 m above sea level and the highest peak among its surrounding mountains is that of the Kolahoi (alt. 5,420 m). The valley is an asymmetrical fertile basin, stretching from South-East to North-Westerly direction. Its diagonal length (from SE to SW corner) is 187 km, while the breadth varies considerably, being 115.6 km along the latitude of Srinagar.

Table 1: Description of the investigated aquatic ecosystems (lakes, wetlands and rivers)

Waterbody	Geographic coordinates Latitude	Longitude	Altitude (m)	Area (km^2)	Depth (m)	Trophic status	Secchi transparency (m)
Standing water ecosystems							
Anchar Lake	34°09'22"	74°47'30"	1584	2.75	1.3	Eutrophic	1.1
Dal Lake	34°07'55"	74°51'21"	1584	10.5	0.9	Eutrophic	0.4
Manasbal Lake	34°14'52"	74º40'07"	1583	2.8	4.5	Low-eutrophic	3.5
Nilnag Lake	33°51'22"	74º41'36"	2180	0.5	5.5	Oligotrophic	4.5
Wular Lake	34°20'08"	74º32'54"	1580	21	3.0	Eutrophic	1.5
Hokersar Wetland	34°06'02"	74º43'08"	1584	7.5	0.7	Low-eutrophic	0.3
Hygam Rakh	34°13'11"	74º32'29"	1586	7.0	2.2	Eutrophic	*
Mirgund Wetland	34°07'32"	74º40'36"	1583	3.0	1.5	Low-eutrophic	*
Shalimar Wetland	34°09'29"	74º52'33"	1611	0.5	1.5	Eutrophic	
Free-flowing ecosystems							
Bijbehara, irrigation canal	33°09'03"	75°06'55"	1597	*	0.8	*	*
Mawas Canal	34°09'33"	75º02'42"	1668	*	0.6	*	*
Shalimar Canal	34°09'02"	74°51'37"	1609	*	1.0	Eutrophic	*
Kolam-Chinar, Anantnag	33°41'28"	75º11'13"	1682	0.05	1.2	*	*
Dodih-Koel	33°36'42"	75°07'37"	1624	*	0.8	*	*
Panzath	33°36'42"	75º10'15"	1705	0.15	0.8	Oligotrophic	*
Lok Bhawan	33°38'26"	75º10'03"	1675	0.06	1.0	*	*
Seasonal pond-type ecosystems							
Khazan-Sar, Kabamrag	33°38'42"	75º09'45"	1676	0.08	0.9	*	*
Daldal-Sar, Kabamarg	33°38'46"	75º09'45"	1675	0.06	0.8	*	*
Ugjan, Dialgam	33°41'13"	75°09'33"	1624	0.06	*	*	*
Alpine aquatic ecosystems							
Bota Pathri, Gulmarg	34°04'15"	74°19'09"	2838	0.04	0.8	*	*
Sinthan Lake	33°34'53"	75°30'39"	3748	0.3	0.9	*	*
Gangabal Lake	34°25'50"	74°55'30"	3600	1.0	1.6	Oligotrophic	*

Systems varied in trophic status along an oligotrophic-mesotrophic-eutrophic gradient within an altitudinal range of 1580-3748 m.a.s.l. *Refers to unavailable data for lakes, wetlands and rivers

Kashmir Valley abounds in an enchanting diversity of aquatic ecosystems, including wetlands, lakes, rivers, springs and streams. These ecosystems vary from alpine lakes to subalpine to temperate and present a gradient of trophic status ranging from some highly eutrophic through mesotrophic to some oligotrophic systems. Aquatic ecosystems located in the pine forest zone of the Pir Panjal, such as Nilnag Lake and those in the Kashmir Valley, exhibit well-developed and stratified vegetation. The high-altitude lakes above 4,000 m in the Pir Panjal Range are largely devoid of macrophyte vegetation.

Exploration and collection of plant material: The freshwater ecosystems of Kashmir Himalaya were extensively surveyed for the period of 03 years w.e.f. March, 2016 to March, 2019 to collect the plant material of aquatic macrophytic species for characterization of the current stage of invasion and clonal growth organ spectra. The sites were selected based on two important criteria, type of aquatic habitats and trophic status. Aquatic ecosystems were classified into four groups mainly based on the habitat type, vegetation and climate. These groups include standing-type ecosystems, free-floating, seasonal pond-type and alpine aquatic ecosystems, the details of the geographical location of the selected sites and the characteristic features are summarized in Table 1. Multiple transects were established to capture the diversity of plant life from the littoral to the limnetic zones of the lake. Along each transect, 30 quadrats of varying sizes, ranging from 0.25-5 m^2, were placed to assess the diversity and plant abundance. For morphological description, optimally several individuals of each plant species were excavated with below-ground organs and preserved using standard herbarium methodology (such as pressing, drying preservation, etc.) for future comparison and identification. The voucher specimens were deposited in the Kashmir University Herbarium (KASH) at the Centre for Biodiversity and Taxonomy, Department of Botany.

Trait selection and clonal growth form categorization: Based on clonality, the plants were divided into clonal plants (if a plant spreads and multiplies clonally i.e., using clonal growth organ (CGO), the species is considered as clonal) and non-clonal plants (reproduce dominantly by sexual methods). For each species, clonal trait data were collected through field studies and laboratory investigations. Besides, using the CLO-PLA 3(Clonal Plant) database of clonal growth in plants various literature sources were used to identify the types of CGOs for each species from the aquatic species pool[20,30]. Based on life form, the plants were categorized as emergent, submerged type, rooted floating type and free-floating type.

Clonal plants are broadly delimited into two categories, namely phalanx and guerrilla. The delimitation is based on a variety of clonal architectural forms (e.g., rhizomes or stolons), branching frequencies and branching patterns. These architectures differ among plant species or within a species in different environments. Target clonal plants were further categorized into four space occupancy strategies based on two characteristics: Rate of lateral spread (spreading non-spreading) and persistence of connections between ramets (splitters-plants producing adventitious roots with main root decaying; integrators-plants not producing adventitious roots and/or with).

Based on nativity plants were delimited into native/or cosmopolitan and invasive alien species. Invasive alien species were further categorized into different stages of invasion which were established based on the current spatial spread of investigated plants following the hierarchical models (CM model) proposed by Calautti and MacIsaac[31]. The total 88 invasive alien species recorded were divided into five stages of invasion (Appendix 1). It is pertinent to mention that the CM model described seven stages of invasion, starting from resident species in a potential donor region (stage 0), carried through different transport vectors (stage I) and released into the introduced region (stage II). The model used abundance and distribution of exotic species in the introduced range, to divide the stages III through V. The invasiveness increases from, stage II up to stage V.

Appendix 1: Data set of aquatic macrophytes in studied aquatic ecosystems to their clonality, space occupancy strategies and stage of invasion

Family/plant species	Growth form	Clonality	Clonal growth organs (CGO's)	Space occupancy strategies	Invasion stage
Alismataceae					
Alisma lanceolatum With.	E	Clonal	9	Non-spreading splitter type	III
Alisma plantago-aquatica L.	E	Clonal	9	Non-spreading splitter type	IVa
Sagittaria latifolia Willd.	E	Clonal	9,12	Non-spreading splitter type	III
Sagittaria sagittifolia L.	E	Clonal	9,12	Non-spreading Splitter type	V
Amaranthaceae					
Amaranthus livid L.	E	Non clonal	-	-	II
Alternanthera sessilis (L.) R. Br. ex DC.	E	Non clonal	-	-	IVb
Apiaceae					
Berula erecta (Huds.) Coville	E	Clonal	9,1,10	Non-spreading splitter type	IVa
Araceae					
Acorus calamus L.	E	Clonal	9	Spreading integrator type	II
Asteraceae					
Bidens cernua L.	E	Clonal	14	Non-spreading integrator type	IVa
Azollaceae					
Azolla sp.	FF	Clonal	5,	Spreading splitter type	IVb
Balsaminaceae					
Impatiens glandulifera Royle	E	Non clonal	-	-	Native*
Boraginaceae					
Myosotis scorpioides L.	E	Clonal	10	Non-spreading integrator type	III
Brassicaceae					
Barbarea intermedia Boreau	E	Clonal	9,15	Non-spreading splitter type	III
Barbarea vulgaris W.T. Aiton	E	Clonal	9,15	Non-spreading splitter type	IVa
Cardamine flexuosa	E	Non clonal	-	-	IVb
Nasturtium officinale W.T. Aiton	E	Clonal	1,5	Spreading splitter type	V
Rorippa islandica (Oeder) Borbás	E	Clonal	10,14,15	Spreading splitter type	IVb
Butomaceae					
Butomus umbellatus L.	E	Clonal	9,13	Non-spreading splitter type	IVb
Callitrichaceae					
Callitriche stagnalis	E	Clonal	1,5	Non-spreading splitter type	IVb
Caryophyllaceae					
Myosoton aquaticum (L.) Moench	E	Clonal	10,1	Non-spreading splitter type	III
Ceratophyllaceae					
Ceratophyllum demersum L.	S	Clonal	2,5	Spreading splitter type	V
Cyperaceae					
Carex diluta Bieb.	E	Clonal	9,12	Non-spreading splitter type	III
Cladium mariscus (L.) Pohl	E	Clonal	9,10	Non-spreading splitter type	III
Cyperus difformis L.	E	Clonal	10,12	Non-spreading splitter type	V
Cyperus fuscus L.	E	Clonal	9	Non-spreading splitter type	IVa
Cyperus iria L.	E	Clonal	9	Non-spreading splitter type	IVa

Appendix 1: Continue

Family/plant species	Growth form	Clonality	Clonal growth organs (CGO's)	Space occupancy strategies	Invasion stage
Cyperus rotundus L.	E	Clonal	10,12	Non-spreading splitter type	IVa
Eleocharis atropurpurea (Retz.) Kunth	E	Clonal	10	Non-spreading integrator type	III
Eleocharis palustris (L.) Roem. & Schult.	E	Clonal	10	Non-spreading integrator type	IVa
Fimbristylis dichotoma (L.) Vahl.	E	Clonal	10	Non-spreading integrator type	III
Scirpus juncoides Roxb.	E	Clonal	10	Non-spreading integrator type	III
Scirpus maritimus L.	E	Clonal	10	Non-spreading integrator type	III
Scirpus triqueter L.	E	Clonal	10	Non-spreading integrator type	III
Haloragaceae					
Myriophyllum verticillatum L.	E	Clonal	2,5	Spreading splitter type	V
Myriophyllum spicatum L.	S	Clonal	10,5	Spreading integrator type	V
Myriophyllum aquaticum (Vell.) Verdc.	E	Clonal	2,5	Spreading splitter type	V
Hippuridaceae					
Hippuris vulgaris L.	E	Clonal	10,5	Spreading integrator type	IVa
Hydrocharitaceae					
Hydrilla verticillata (L.f.) Royle	S	Clonal	2,10,12	Spreading splitter type	V
Hydrocharis dubia (Blume) Backer	RF	Clonal	1,2	Spreading splitter type	V
Vallisneria spiralis L.	RF	Clonal	1,9	Spreading integrator type	II
Juncaceae					
Juncus articulatus L.	E	Clonal	10,1,4	Non-spreading splitter type	IVa
Juncus bufonius L.	E	Clonal	4,5,9	Non-spreading splitter type	III
Juncus effusus L.	E	Clonal	10	Non-spreading splitter type	IVa
Juncus inflexus L.	E	Clonal	10	Non-spreading splitter type	II
Labiatae (Lamiaceae)					
Mentha aquatica L.	E	Clonal	10,5,1	Spreading splitter type	III
Mentha longifolia (L.) Huds.	E	Clonal	10	Spreading integrator type	V
Mentha piperita L.	E	Clonal	10	Spreading integrator type	IVa
Lycopus europaeus L.	E	Clonal	10,12	Spreading integrator type	V
Lemnaceae					
Lemna gibba L.	FF	Clonal	2,6	Spreading splitter type	V
Lemna minor L.	FF	Clonal	2,6	Spreading splitter type	V
Lemna trisulca L.	FF	Clonal	2,6	Spreading splitter type	IVb
Spirodela polyrhiza (L.) Schleid.	FF	Clonal	2,6	Spreading splitter type	IVa
Wolffia arrhiza (L.) Horkel ex Wimm.	FF	Clonal	2,6	Spreading splitter type	IVa
Lentibulariaceae					
Utricularia aurea Lour.	S	Clonal	2,5	Spreading splitter type	IVb
Lythraceae					
Ammania auriculata Wild.	E	Non clonal	-	-	III
Ammannia baccifera L.	E	Non clonal	-	-	III
Lythrum salicaria L.	E	Clonal	10,5,14	Spreading splitter type	IVa
Marsileaceae					
Marsilea quadrifolia L.	RF	Clonal	1,10	Spreading splitter type	V
Menyanthaceae					
Menyanthes trifoliata L.	E	Clonal	5,9	Spreading integrator type	III
Nymphoides peltata (S.G.Gmel.) Kuntze	RF	Clonal	9,10	Spreading splitter type	V
Najadaceae					
Najas marina L.	S	Clonal	2,5	Spreading splitter type	III
Nelumbonaceae					
Nelumbo nucifera Gaertn.	RF	Clonal	10	Spreading integrator type	IVb
Nymphaeaceae					
Nymphaea alba L.	RF	Clonal	10,16	Spreading splitter type	IVb
Nymphaea lotus L.	RF	Clonal	10,16	Spreading splitter type	III
Nymphaea tuberosa Paine.	RF	Clonal	10,16	Spreading splitter type	III
Euryale ferox Salisb.	RF	Clonal	10	Non-spreading integrator type	Native*
Onagraceae					
Epilobium hirsutum (L.) Gray	E	Clonal	10	Non-spreading splitter type	V
Epilobium palustre L.	E	Clonal	10,13	Non-spreading splitter type	III
Orchidaceae					
Spiranthes lancea (Thunb.) Baker	E	Clonal	9,16	Non-spreading splitter type	II

Appendix 1: Continue

Family/plant species	Growth Form	Clonality	Clonal growth organs (CGO's)	Space occupancy strategies	Invasion stage
Poaceae					
Echinochloa colonum (L.) Link.	E	Clonal	9	Non-spreading splitter type	III
Echinochloa crus-galli (L.) P.Beauv.	E	Clonal	9	Non-spreading splitter type	IVa
Phalaris arundinacea L.	E	Clonal	10,5	Spreading integrator type	III
Phragmites australis (Cav.)	E	Clonal	1,5,10,9,17	Spreading integrator type	V
Polygonaceae					
Polygonum hydropiper L.	E	Clonal	9	Non-spreading splitter type	V
Polygonum amphibium L.	RF	Clonal	10,5	Spreading splitter type	IVb
Polygonum lapathifolia (Linn.)	E	Non Clonal	-	-	Native*
Polygonum nepalense Meisn.	E	Non Clonal	-	-	Native*
Rumex aquaticus L.	E	Clonal	9,14	Non-spreading splitter type	III
Rumex conglomeratus Murray	E	Clonal	14	Non-spreading splitter type	V
Rumex dentatus L.	E	Clonal	14	Non-spreading Splitter type	IVa
Potamogetonaceae					
Potamogeton crispus L.	S	Clonal	2,10,12	Spreading splitter type	V
Potamogeton natans L.	RF	Clonal	5,10	Spreading splitter type	IVb
Potamogeton nodosus Poir.	RF	Clonal	2,10,12	Spreading splitter type	V
Potamogeton lucens L.	S	Clonal	2,10,12	Spreading splitter type	IVb
Potamogeton pectinatus L.	RF	Clonal	2,3,5,10	Spreading splitter type	IVb
Potamogeton perfoliatus L.	S	Clonal	5,10,12	Spreading splitter type	III
Potamogeton pusillus L.	S	Clonal	2,5,10	Spreading splitter type	III
Potamogeton wrightii Morong	S	Clonal	10,12	Spreading splitter type	Native*
Ranunculaceae					
Ranunculus muricatus L.	E	Non clonal	-	-	Native*
Ranunculus sceleratus L.	E	Non clonal	-	-	Native*
Caltha alba K. Jacq	E	Clonal	5,9	Non-spreading integrator type	Native*
Ranunculus lingua L.	E	Clonal	9,12	Spreading integrator type	III
Ranunculus trichophyllus Chaix	RF	Clonal	1,5	Spreading integrator type	Native*
Rosaceae					
Potentilla reptans Linn.	E	Clonal	1,9	Spreading integrator type	Native*
Rubiaceae					
Galium aparine L.	E	Non Clonal	-	-	Native*
Salviniaceae					
Salvinia natans All.	FF	Clonal	5	Spreading splitter type	V
Scrophulariaceae					
Veronica anagallis-aquatica L.	E	Clonal	14	Non-spreading splitter type	Native*
Veronica beccabunga L.	E	Clonal	14	Non-spreading splitter type	Native*
Sparganiaceae					
Sparganium erectum Huds	E	Clonal	9,10,12	Spreading integrator type	V
Trapaceae					
Trapa natans L.	RF	Clonal	1,5	Spreading splitter type	V
Typhaceae					
Typha angustata Bory & Chaub.	E	Clonal	10,12	Spreading integrator type	V
Typha laxmannii Lepech.	E	Clonal	10,12	Spreading integrator type	III

*Refers that some species categorized as native are cosmopolitan in distribution. CGO's Reported; 1: Horizontal above-ground stem, 2: Turion, 3: Bulbil and tuber of stem origin at or above soil surface, 4: Plantlet (pseudovivipary), 5: Plant fragment of stem origin, 6: Budding plant, 9: Epigeogenous stem (rhizome), 10: Hypogeogenous stem (rhizome), 12: Stem tuber, 13: Bulb, 14: Root-splitter, 15: Roots with adventitious buds, 16: Root tuber and 17: Offspring tuber at distal end of above-ground stem. Life forms; E: Emergents, S: Submerged, RF: Rooted floating and FF: Free floating. Invasion stages; Stage II: Species at introduction phase, Stage III: Species localized and numerically rare, Stage IV: Widespread in distribution but rare in number, Stage Iva: Localized but dominant and Stage V: Dominant species with severe damage to local diversity

Nativity of species: Geographic affiliations and nativity of the species were established through standard sources, such as Atlas Florae Europaeae[6,32]. In addition, some relevant web sources of the Germplasm Resource Information Network (GRIN), the United States Department of Agriculture (USDA) and the Integrated Taxonomic Information System (ITIS) were also used.

Data analysis: The relationship between clonality and plant invasion was worked out employing Spearman's rank correlation. The invasive alien species recorded during the study were divided into five groups based on the degree of invasiveness ordinally. The invasiveness increases from group I-V. The first group (stage II) consists of those species that are just in the introduction phase and have not yet adopted well in the non-native region. The second group (stage III) includes those species that are localized and numerically rare. The third group (stage IV) contains those species that are widespread in distribution but rare in number. The fourth group (stage IVa) consists of species localized but dominant. The fifth group (stage V) consists of those species that occupy extensive areas and are dominant with severe damage to local diversity. Most of stage-V species have been listed in the World's Worst Invasive Alien Species. To study the relationship between clonality and trophic status, cluster mean analysis was carried out. The statistical analysis was done using R Static software (R-2.15.2 for Windows, Standard Version).

RESULTS

Clonal growth form categorization: Out of 101 total plant species recorded in all investigated aquatic ecosystems 91 species were clonal and only 10 were non-clonal. Categorization of the clonal species into 14 clonal growth forms (Fig. 1) showed that the epigeogenous (originated above-ground) and the hypogeogenous (originated below-ground) rhizomes are the most common CGOs in the Kashmir Himalayan aquatic ecosystems, each reported in 44 and 33 species, respectively. The other dominant clonal growth forms found in the study species were plant fragments of stem origin; turion and stem tubers.

The amplitude of clonal growth organs (CGO's) within species varies as several species show regeneration by more than one type of CGO's and others by a single type of CGO's. Based on these observations clonal plant species were classified into different categories i.e., species with a single type of CGO were designated as uni-modal (1 modal), those with two types of CGO's as bi-modal (2 modal) and so on. The highest numbers of species were found to be bi-modal followed by uni-modal type (Fig. 2). The target species were further sub-grouped into four space occupancy strategies. Classification of space occupancy strategies revealed that a quarter of the species are non-spreading splitters (33%) followed by spreading splitters (31%), non-spreading integrators (15%) and spreading integrators (11%) (Fig. 3).

Clonal growth spectra: The freshwater ecosystems support a definite type of vegetation ranging from submerged, attached floating, free-floating and emergent aquatic grasses, herbs, reeds and sedges. The proportion of the different growth forms in all studied ecosystems showed a predominance of clonality (91%) over non-clonality (Fig. 4). In all the studied aquatic ecosystems there is evident variability in several species and clonal growth organ spectra. The lowest number of species and clonal growth organs (CGO's) were reported in alpine lake ecosystems, while the highest number was reported in a standing type of ecosystems. Seasonal-type ecosystems having intermediate plant diversity usually supported species belonging to an emergent type of life form while in standing water-type ecosystems all life forms were well represented (Table 2). The results of Agglomerative Hierarchical Clustering (AHC) based on clonal architecture showed that seasonal pond-type ecosystems, free-flowing type ecosystems and standing-type ecosystems have a higher degree of similarity, while the alpine aquatic ecosystems showed the least level of similarity with the rest three types of ecosystems. This is because alpine aquatic ecosystems favor only integrator type of clonal architectures which are resistant to harsh environmental conditions.

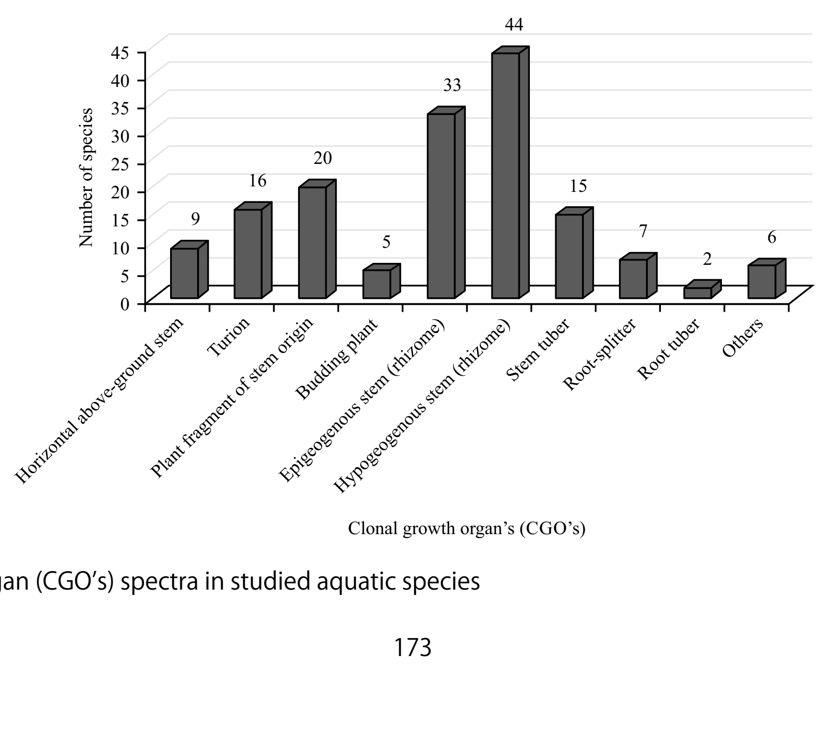

Fig. 1: Clonal growth organ (CGO's) spectra in studied aquatic species

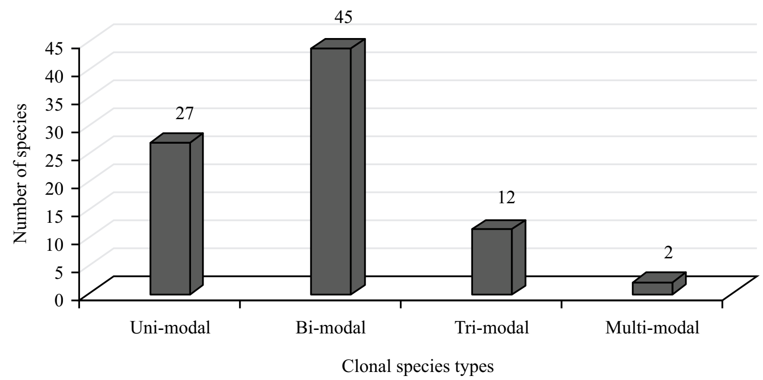

Fig. 2: Number of aquatic plant species with varied modes of clonal propagation in Kashmir Himalaya

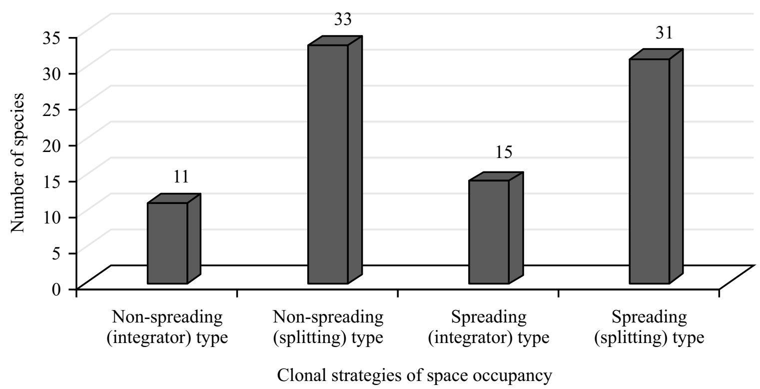

Fig. 3: Number of aquatic plant species with different space occupancy strategies

Table 2: Clonal richness and species composition of studied aquatic ecosystems

Aquatic ecosystems	Clonal growth organ richness	Species reported	Clonal species	Non-clonal species	Dominant families
Standing water ecosystems	14 CGO's	100	89	11	Cyperaceae (12 species) Polygonaceae (7 species) Potamogetonaceae (7 species) Lemnaceae (5 species)
Free-flowing ecosystems	11 CGO's	56	49	7	Cyperaceae (10 species) Polygonaceae (5 species) Potamogetonaceae (4 species) Lemnaceae (3 species)
Seasonal pond-type ecosystems	10 CGO's	37	31	6	Cyperaceae (5 species) Polygonaceae (4 species) Lemnaceae (3 species) Ranunculaceae (3 species)
Alpine aquatic ecosystems	3 CGO's	3	3	0	Ranunculaceae (2 species)

Table 3: Distribution of target species at various stages of invasion in all investigated Kashmir Himalayan water bodies into various clonal growth organ groups

			Clonal plants						
Invasiveness	Total number	Total number	Number of species with A	Number of species with B	Number of species with C	Number of species with D	Number of species with E	Number of species with F	Number of species with other CGO's
Group I	5	4	1	0	0	3	1	0	1
Group II	28	26	2	2	7	10	16	5	6
Group III	17	17	1	2	2	6	8	1	5
Group IV	14	12	1	4	5	9	7	1	5
Group V	24	24	4	8	6	5	12	8	2
Total	88	83	9	16	20	33	44	15	18

A plant species can have multiple clonal organs. CGO's: A: Horizontal above-ground stem, B: Turion, C: Plant fragment of stem origin, D: Epigeogenous stem (rhizome), E: Hypogeogenous stem (rhizome), F: Stem tuber, O's: Other types. Life forms; Emr: Emergents, Sb: Submerged, R.F: Rooted floating and F.F: Free floating

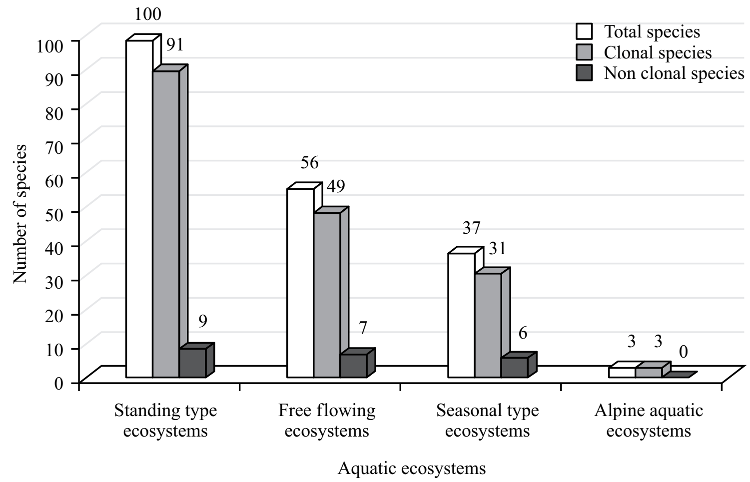

Fig. 4: Proportion of clonal and non-clonal species in target aquatic ecosystems

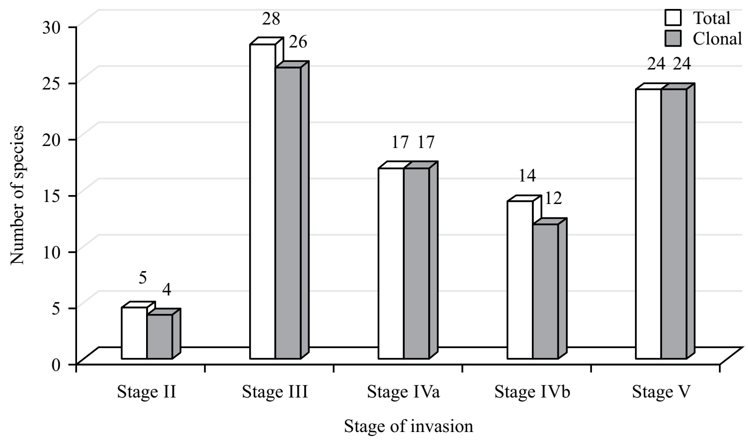

Fig. 5: Extent of clonality in alien aquatic plant species of different invasion stages in the Kashmir Valley

Clonality and invasiveness: Across all groups, 88 species were recorded, 83 of which were clonal (Fig. 5). The most utilized CGOs were E (44 species) and D (33 species), followed by C (20 species), "Other CGOs" (18 species) and F (15 species). The CGOs B and A were the least utilized, found in 9 and 16 species, respectively.

Clonal plants accounted for 94% of total alien invasive species and it was interesting to note that all stage V species were clonal (Fig. 6). Categorizing alien plant species into a phalanx and guerrilla strategies of space occupancy showed that among highly invasive plant species (stage V) 19 out of 24 are guerrilla type which favors their predominance in all aquatic ecosystems (Fig. 6). A significant positive correlation between clonality and invasiveness ($p<0.005$) was found (Table 4). In particular, clonal species with turion, plant fragment of stem origin and hypogeogenous stem (rhizome) showed significant positive correlations with invasiveness.

Clonal growth organ spectra about trophic status: A comparative study carried out in water bodies at different trophic statuses showed the least significant distribution pattern of clonal growth organs. Along trophic status, only the abundance pattern of clonal growth organs varies effectively. Using K-mean cluster analysis, a profile plot of clonal growth organs based on abundance data in four study sites belonging to different trophic was obtained (Fig. 7). The result showed that hypogeogenous rhizomes type are most abundant followed by plant fragments of stem origin in eutrophic water bodies. In contrast, root tuber (CLLO 16) and offspring tuber at a distal end of above-ground stem (CLO 17) were absent from oligotrophic lakes. It was also interesting to note that there was the least difference in clonal growth organ spectra in eutrophic and low-eutrophic water bodies while eutrophic and oligotrophic are highly distinct (Table 5).

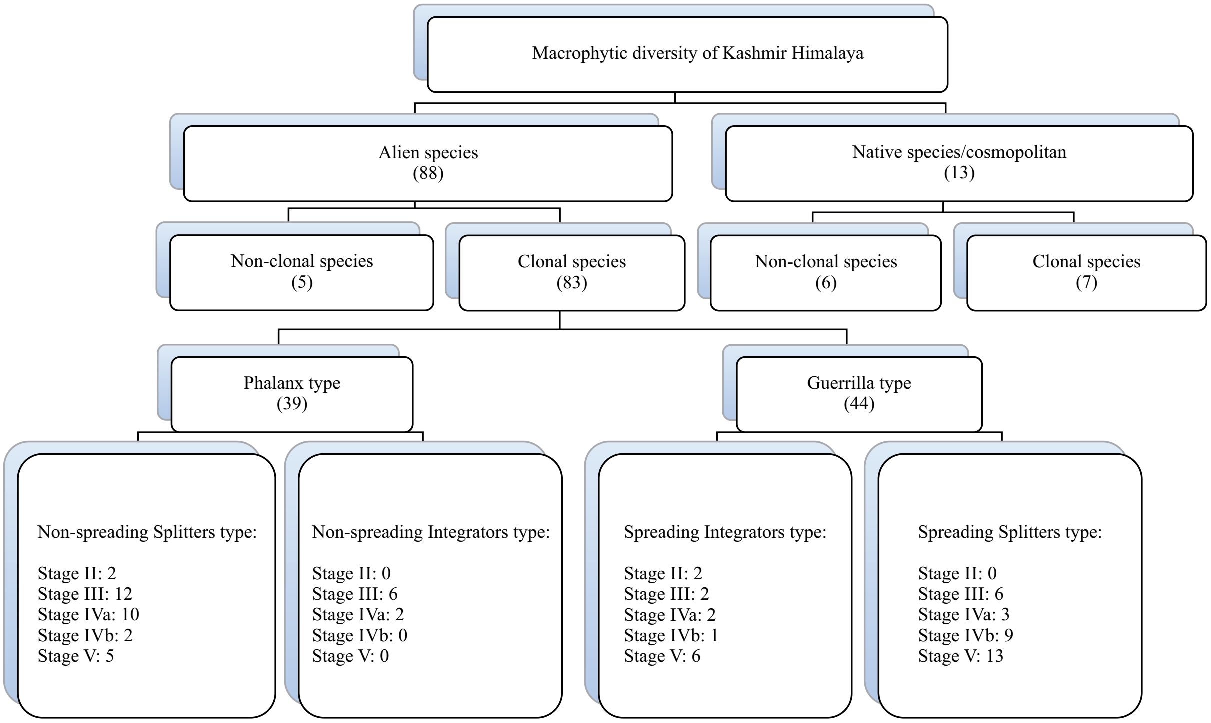

Fig. 6: Flow chart of macrophytic diversity of Kashmir Himalaya

Table 4: Spearman's correlation analyses based on clonality and life form for 88 aquatic alien invasive plant species in Kashmir Himalaya

			CGO's							Life forms		
r	Invasiveness	Clonality	A	B	C	D	E	F	O's	Emr	Sb	R.F
Invasiveness												
Clonality	1.0*											
CGO's												
A	0.88*	0.88*										
B	0.66^{ns}	0.66^{ns}	0.77^{ns}									
C	0.94*	0.94*	0.88*	0.75^{ns}								
D	0.77^{ns}	0.77^{ns}	0.51^{ns}	0.55^{ns}	0.82^{ns}							
E	1.0*	1.0*	0.88*	0.66^{ns}	0.94*	0.77^{ns}						
F	0.92*	0.92*	0.95*	0.86^{ns}	0.92*	0.63^{ns}	0.92*					
O's	0.81^{ns}	0.81^{ns}	0.5^{ns}	0.51^{ns}	0.81^{ns}	0.98*	0.81^{ns}	0.64^{ns}				
Life forms												
Emr	0.8^{ns}	0.8^{ns}	0.00^{ns}	0.6^{ns}	0.87^{ns}	0.82^{ns}	0.8^{ns}	0.6^{ns}	0.2^{ns}			
Sb	0.97*	0.97*	0.67^{ns}	0.97*	0.94*	0.57^{ns}	0.97*	0.66^{ns}	0.0^{ns}	0.71^{ns}		
R.F	0.66^{ns}	0.66^{ns}	0.97*	0.82^{ns}	0.55^{ns}	0.02^{ns}	0.66^{ns}	0.35^{ns}	-0.10^{ns}	0.10^{ns}	0.28^{ns}	
F.F	0.66^{ns}	0.6^{ns}	0.08^{ns}	0.66^{ns}	0.63^{ns}	0.89*	0.66^{ns}	0.97*	-0.10^{ns}	0.71^{ns}	0.70^{ns}	0.32^{ns}

*$p<0.05$, ns: Not significant, CGO's; A: Horizontal above:ground stem, B: Turion, C: Plant fragment of stem origin, D: Epigeogenous stem (rhizome), E: Hypogeogenous stem (rhizome), F: Stem tuber, O's: Other types, Life forms; Emr: Emergents, Sb: Submerged, R.F: Rooted floating and F.F: Free floating

Table 5: Distances between the central objects (trophic status) using K-mean cluster analysis

	1 (Eutrophic)	2 (Low eutrophic)	3 (Mesotrophic)	4 (Oligotrophic)
1 (Eutrophic)	0	88.679	379.907	428.810
2 (Low eutrophic)	88.679	0	354.884	394.137
3 (Mesotrophic)	379.907	354.884	0	126.361
4 (Oligotrophic)	428.810	394.137	126.361	0

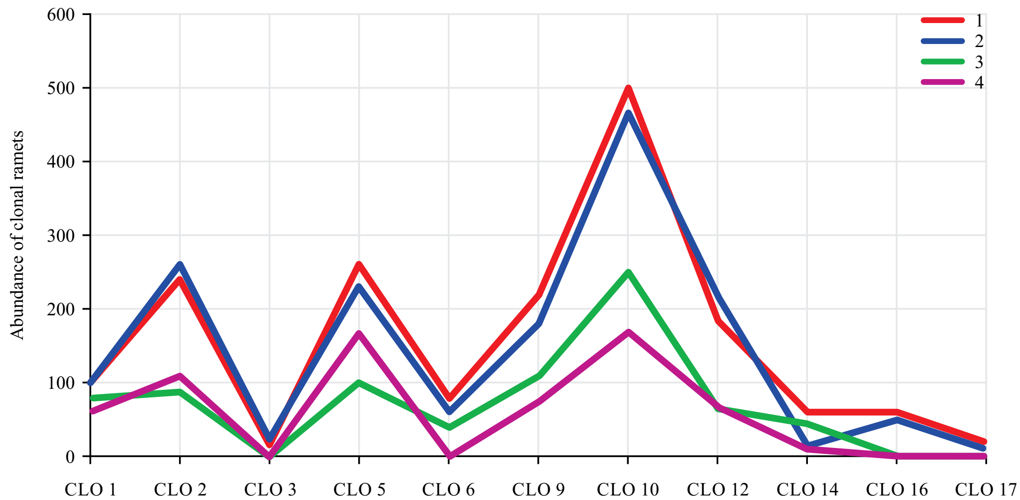

Fig. 7: Profile plot showing the proportion of clonal growth organs in water bodies belonging to different trophic status, using K-mean cluster analysis

DISCUSSION

The present analysis revealed distinct differences between invasive and non-invasive species in traits associated with resource allocation, spatial spread and regeneration. The Kashmir Himalayan aquatic ecosystems showed a significant disparity in the distribution of clonal versus non-clonal invasive plants both in abundance and spatial spread. Understanding the traits that drive plant invasiveness is crucial in the field of invasion biology. Identifying invasive species based on their functional traits is essential for developing effective risk assessment protocols, which are fundamental for managing and preventing plant invasions[33]. The result highlighted that 83 species out of 88 alien species are clonal, these findings strongly suggest that clonality may play a direct role in the higher prevalence and dominance of invasive species in aquatic habitats. The data revealed a significant positive correlation ($p<0.05$) between clonality and invasiveness.

Some previous studies corroborate with the present study, for example, Lavoie *et al.*[34] suggested that the rapid dispersal of propagules by flowing river waters are the well-known corridors of invasive species. The role of clonality in the invasiveness of alien plants demonstrated after initial colonization of a site by seedlings or asexual propagules. Clonal growth seems to be the primary method of maintaining and expanding natural populations for aquatic clonal species[26,28].

During the present study, 14 clonal growth forms and four space occupancy strategies were distinguished in the aquatic angiosperms responding to multiple environmental gradients, especially moisture. Non-spreading integrators and splitters prevailed in growing emergent types of swampy areas (unstable substrate); in submerged types and free-floating types spreading splitters prevailed (plants with long hypogeogenous rhizomes). The spreading integrator strategy was not formed in the free-floating type but was most dominant in the rooted floating and emergent type. The most prevalent clonal growth organs in the Kashmir Himalayan aquatic ecosystems were hypogeogenous rhizomes, followed by epigeogenous rhizomes, stem-origin plant fragments, turions and stem tubers. These observations align with findings reported in the flora of the Czech Republic[20].

Similarly, the ratio between epigeogenous and hypogeogenous rhizomes differed in waterlogged aquatic ecosystems. These findings are consistent with previous reports suggesting that waterlogged soils in wetland habitats may be more conducive to the longer internodes of hypogeogenous rhizomes compared to the soils of terrestrial habitats[5]. On the other hand, there was a lower proportion of root-splitting and root-sprouting species in wetland habitats, which had been reported earlier[28]. This underrepresentation may be caused by the costly maintenance of extensive root systems and a lower R/S (root/shoot) ratio in nutrient-rich conditions, where nutrients can be acquired directly from water[35].

Across all study areas along the altitudinal gradient, despite a significant decline in aquatic species, clonal integrators were found at significantly higher mean and maximum altitudes compared to non-clonal plants and clonal splitters. This contrasts with one of the earlier findings in which they observed no difference in temperature indicator values between clonal plants with short- and long-lived spacers[21]. The dominant presence of integrators at high altitudes is attributed not only to their nutrient economy in nutrient-poor and patchy environments but also to their ability to store carbon in spacers and efficiently utilize it during the short growing season[36].

Along trophic status, only the abundance pattern of clonal growth organs varies effectively. Thus highly invasive aquatic plant species using guerrilla strategies of space occupancy increase in biomass in highly eutrophic lakes and result in the formation of monotypes. Even though there are no earlier records in this field that support or contradict our findings, some indirect observations have shown that there is a preponderance of clonally growing species in nutrient-rich aquatic ecosystems. The wetlands surrounded by agriculture or urban development are often subject to increased surface runoff and eutrophication due to elevated levels of N, P or N+P which in turn enhance the spread of some clonal species[37,38]. Keser *et al.*[39] experimentally showed that invasive clonal plant species exhibited a significantly stronger belowground foraging response compared to non-invasive species, especially in nutrient-rich patches versus nutrient-poor ones. This foraging behavior is likely a manifestation of adaptive phenotypic plasticity[40]. The present study supported the notion that the potential for pronounced phenotypic plasticity contributes to plant invasions. The findings of this study offer valuable insights for managing aquatic invasions and formulating evidence-based ecological conservation strategies. However, the study's short duration, focused solely on the Kashmir Himalayan ecosystems, may not fully capture the long-term dynamics of clonal species and their invasions. Further research is required to assess clonal behavior across diverse ecological conditions.

CONCLUSION

Clonality is an important yet often overlooked trait linked to plant invasiveness in diverse ecosystems especially, aquatic habitats. The present study highlighted clonality's role in the regeneration and spread of alien aquatic plants, particularly highly invasive species that form monotypic stands, dominating invaded ecosystems. Clonality significantly impacts species abundance patterns, with different clonal architectures reflecting distinct foraging strategies: The phalanx strategy exploits local patches, while the guerrilla strategy explores new ones. The present study predicted that species-poor communities, like alpine ecosystems, are especially vulnerable to invasion due to clonality's advantage in harsh environments. More focused field and experimental studies are needed to identify functional traits that promote plant invasions.

SIGNIFICANCE STATEMENT

The invasion of ecosystems by non-native plants has become a big problem for the global environment. Clonal growth has been pointed out as an attribute that could contribute to the invasiveness of plants. The present study was carried out to map the clonal growth spectra of aquatic macrophytes of Kashmir Himalaya and their role in invasiveness. Findings from the present study depict that highly invasive species dominantly used clonal growth organs for spatial spread and regeneration. To enhance understanding and management of invasive species, further research should focus on the adaptive mechanisms of clonal traits, including their role in resource acquisition, resilience to environmental stresses and competitive interactions, as well as the development of targeted strategies to control clonal invaders in sensitive and pristine ecosystems.

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