Clonality in invasive alien macrophytes in Kashmir Himalaya: a stage-based approach

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Abstract
While the link between clonality and species invasiveness has recently been recognized, whether and how clonality vary with different invasion stages remains open questions. Hence, we tested the relationship between clonality and species invasiveness of Kashmir Himalayan aquatic macrophytes vis-à-vis its variability along different stages of invasion. The data on clonality, stage of invasion and growth form were obtained through an extensive survey of literature and database like CLOPLA and PLADIAS followed by evaluation of the clonal organs through intensive field surveys undertaken over a period of 3 years (2014–2017) in different aquatic habitats of the Kashmir valley. Our results showed that 84% of the studied species and almost 90% of the most invasive species (stage V sensu Colautti and MacIsaac: Divers Distrib 10(2):135–141, 2004) are clonal. A highly significant positive correlation between clonality and invasiveness was observed, which further substantiates this association at a broad geographical scale representing the whole region. The distinction of clonal growth forms and significant positive correlation between clonality and different clonal growth organs (rhizomes, runners and turions) further affirm the strong nexus of clonality with species invasions. Future studies directed at unraveling the reasons behind clonality need to be undertaken from the genomic perspective, in order to develop better means for proper management of alien aquatic invasive species.

Keywords Clonality · Clonal growth organs · CLO-PLA · Growth form · Kashmir Himalaya · PLADIAS · Plant invasion

Introduction
The rapid spread of invasive alien plants, overrunning the habitats of native species, causes enormous economic and ecological damage (Schmitz and Simberloff 1997; Mack et al. 2000). For instance, *Myriophyllum spicatum* (water milfoil), an aquatic macrophyte, in Lake Tahoe of Sierra Nevada (United States), caused a loss of US$500 000 annually (Eiswerth et al. 2005; Pejchar and Mooney 2009). In Wular Lake, Asia’s one of the largest freshwater lakes, Alligator weed (*Alternanthera philoxeroides*) forms dense floating patches that block light penetration to lower strata, creates high biological oxygen demand and promotes sedimentation and flooding (Keller et al. 2018). The invasive alien species change ecosystem dynamics by effecting ecosystem structure and functioning, including reduction in native species diversity, modification of soil nutrient pools and fluxes, and alteration of ecosystem productivity (Liao et al. 2008; Pyšek et al. 2002; Barney et al. 2015; Khan et al. 2021).

Invasive species are thought to be successful in their introduced environments because they occupy novel or empty ecological niches, and/or they possess fitness differences that drive competitive dominance over resident communities (McDougall et al. 2009). Invasive plant species also impose new selective pressures on native species which may result in evolutionary changes in some native species, reducing competitive exclusion and allowing for coexistence with the invader (Zenni et al. 2017). The ecosystem of low resistance and less managed natural resources is found to be prone to change their species abundances and compositions...
due to increased invasions (McNeely 2001), which further deteriorates these ecosystems by forming monotonous mats on water surface, thereby preventing the light penetration, decreasing dissolved oxygen and declining phytoplankton productivity. Being a rich provider of a wide-ranging variety of ecosystem services and goods, the fresh water biodiversity is progressively threatened by extensive resource exploitation, habitat degradation, water flow changes, pollution (Dudgeon et al. 2006) but invasion of alien species appears to impact the ecosystem most severely (Zedler and Kercher 2004; Olden 2006), thereby creating unfavorable conditions for the native species by strongly modifying local factors (Urban et al. 2006; Pierobon et al. 2010; Andersen et al. 2017; Vilas et al. 2017). Moreover, many aquatic plants have a huge potential of quickly increasing their spatial distribution, thus making them characteristically invasive (Richardson et al. 2000).

The mountainous region of Kashmir Himalaya harbors 3813 wetlands and water bodies (Romshoo and Sumira 2010), which have been studied for various aspects of biodiversity, environmental status in terms of hydrology (Khan et al. 2004), limnology (Zutshi et al. 1980), trophic structure (Pandit and Kaul 1982), food chain structure (Pandit 1980), but the role of clonality in aquatic plant invasion has received very scanty attention (Bashir Shah et al. 2014, b). A disproportionate fraction of aquatic plant species reproduces vegetatively mainly due to the possession of a wide range of clonal growth organs (Grace 1993; Boedeltje et al. 2004; Combroux and Bornette 2004; Dorken and Barrett 2004). Competitive interactions occur between the invasive and native species, where former generally outcompete the native species of the resident community, resulting in a successful invasion (Funk and Vitousek 2007; Davidson et al. 2011; Pearse and Altermatt 2013; Kuebbing and Nuñez 2016). What determines alien invasive species dominance over native plant species is still little known, but there is an emerging pattern that many of the world’s worst invasive plants are successful invaders due to the significant connection between their clonal traits and invasiveness (Song et al. 2013; Wang et al. 2017).

Clonality is a form of plant growth that results in the production of genetically identical individuals capable of independent growth and reproduction. New individuals are formed by clonal propagation from specialized organs called as clonal organs (Harper 1977).

Aquatic plants display a remarkable range of reproductive strategies, including diverse sexual systems and means of clonal propagation (Barrett et al. 1993). There are conflicting views on whether or not certain reproductive adaptations are of special value to weedy species. Variation in reproductive traits will influence the ability of populations to colonize and persist in different types of aquatic habitats and probably vast majority of weeds are self-compatible or possess strong powers of vegetative reproduction (Baker 1955). Baker feels that these characteristics are of importance in the long-distance dispersal of weeds. Therefore, the question being asked here is whether clonal traits (clonal organs) associated with alien invasive clonal plants help them to dominate over native plants.

Asexual reproduction in clonal plants provides several ecological benefits compared to sexual reproduction. These benefits include the ability of clones to acquire different resources from multiple sites through horizontal organs (Evans and Cain 1995), store nutrients in below-ground clonal architecture for long-term persistence in cold environments (Venn and Morgan 2009), increase the ability of clonal propagates to disperse to new environments, intra-clonal resource sharing among ramets in response to resource heterogeneity (Alpert and Stuefer 1997), opportunities for physiological integration and spatial division of labor between ramets; and clonal integration can increase the fitness of performance-related clonal traits and thus can multiply rapidly and compete effectively over non-clonal plants (Van Groenendael et al. 1996; de Kroon et al. 1998). Importantly, clonal reproduction provides a safe alternative to risky seed production and recruitment (Callaghan and Emanuelsson 1985). Consequently, clonal reproduction is thought to play an important role in population persistence and conservation in hostile environmental conditions (Grace 1993), and a significantly higher proportion of clonal reproduction have been observed to occur in cold environmental conditions than in temperate environments (Klimeš and Stamatí et al. 2007). Clonal growth serves as a reproductive insurance mechanism that further affects plant demography and possible evolutionary rates (Klimešová et al. 2021). Asexual reproduction in clonal plants also provides several evolutionary benefits, including the gain of advantage by avoiding the costs associated with sexual reproduction and a means by which clonal species can be rapidly adapted after colonization to the new environments they face (Barrett 2015). Clonal plants often persist for longer periods in habitats in which sexual reproduction is prevented, either because of the absence of mating partners, or where environmental conditions are not favorable for seed germination, seed set, or seedling establishment (Barrett 2015).

Clonal integration has been suggested to contribute to the global invasiveness of clonally growing plants from the results of a recent meta-analysis, in which the link between degree of invasiveness and clonal integration of about 60 clonal plants was examined (Song et al. 2013). A large proportion of plant species is clonal (Grace 1993; Klimeč and Klimešová 1999; Sosnová et al. 2011), consisting of network of cloned individuals connected by large network of below-ground spacers mostly by rhizomes and stolons (Sosnova et al. 2010; Xu et al. 2012). In contrast to non-clonal plants, clonal plants have additional features in terms of number of
ramets (root-shoot unit), branching pattern of clonal organs, such as rhizomes, and stolon and the spacer length between ramets (Callaghan et al. 1990; Huber et al. 1999; Ikegami et al. 2007). The potential of alien species to invade new areas may be predicted from the influence of their native region (Reichard 2001) and similarity in the environmental conditions between native and invaded regions favors the plant invasion. If the species has a large native geographical area, the possibility of transfer of its propagules increases to the region with a similar climate (Mihulka and Pyšek 2001; Shah et al. 2012). The aquatic flora of Kashmir Himalaya was recently compiled and all the species were characterized on the basis of different invasion stages, in accordance with the CM model proposed by Colautti et al. (2004). The CM model describes seven stages (0, I, II, III, IVa, IVb, and V) which are reflective of the sequential series of steps involved in the process of biological invasions. The process of invasion begins as propagules in the existing donor region (stage 0), pass through a series of barriers that may prevent their transition to subsequent stages, some of which are taken into the transport vector (stage I), usually by humans. The surviving propagules transport and release to become introduced (stage II), they have the potential to establish (stage III) in a novel environment where they become widespread (stage IVa) or dominant (stage IVb), and widespread and dominant (stage V).

The CM model has been successfully tested by some workers (Lawes et al. 2006; Shah et al. 2012), though more studies need to test the model for its robustness and wide-scale applicability to take it forward from its stage of scientific infancy.

In view of lack of information about whether or not aquatic alien species at different stages of invasion exhibit any significant relation with clonality, the specific question addressed in this study was whether there is any relationship between clonality and invasiveness in aquatic macrophytes and how does it vary along different stages of invasion? We used 102 major invasive alien plant species found in the aquatic habitats of Kashmir Himalaya and representing different life forms, invasion stages and clonal organs for this purpose.

Materials and methods

Study area

With a large biogeographic domain, the valley of Kashmir is situated in the north-western Himalayas (Rodgers and Panwa, 1988). The region comes under coordinates of (33° 22' and 34°50' N latitudes and 73°55' and 73°33' E longitudes), covering an area of about 16,000 km², with about 64% of the total area is comprised of mountains (Ganaie et al. 2014). The valley is a deep elliptical bowl-shaped surrounded by a girdling chain of high mountain ranges, namely the PirPanjal in the south and southwest, and the Zanskar, the Greater Himalayan range in the north and northeast.

Also, the valley of Kashmir has a network of numerous glaciated streams, lakes, springs, rivers as well as alpine, sub-alpine, and freshwater ecosystems along an altitudinal gradient, mainly due to its unique edaphic characteristics, eco-climatic conditions, and geographical location, together with its undulating topography and lofty snow-capped mountains and hills.

Data collection

We targeted the aquatic flora of Kashmir Himalaya with special reference to lakes and wetlands for the present study. At the beginning, information about the occurrence, distributional range, invasiveness, clonality, origin, growth form, life form, and stages of invasion was obtained through extensive screening of available literature such as specimens of the targeted flora that were stored in the Kashmir University Herbarium (KASH), published research articles, weed floras, etc. The most valuable sources of information about the presence of aquatic invasive species among different habitats were pursued (Kaul et al. 1976; Naqshi 1981; Kak 1984, 1990; Reshi 1984; Koul and Naqshi 1988; Khan et al. 2004; Shah et al. 2014a; Shah and Reshi 2014; Wani et al. 2018; Kaul 2019). Pursuant to useful information gained through the study of previous literature, we followed up with thorough field surveys undertaken for a period of 3 years (2014–2017), in different aquatic habitats of the Kashmir valley. Species were grouped in invasion stages based on the extent of spatial spread in the Kashmir Himalayan region, measured in terms of the density and abundance across sites in the framework of the CM model.

The field data were collected during seasonal surveys in the target water bodies. During the survey, a total of 125 species were recorded from 9 lakes, 5 wetlands, 7 streams, and 2 rivers. Out of them, 102 species were included in the present study, while the remaining 23 species were excluded because of insufficient information (Online Appendix 1). A total of 2300 (1 m²) quadrates were laid randomly (100 in each water body) across different zones (littoral, marsh, open waters) to take into account maximum macrophyte diversity for the present analysis.

Each species was ascertained whether it is a clonal or non-clonal plant. All the clonal species were evaluated for their clonal organs (Online Appendix 1). We evaluated the clonal organs after the flowering and fruiting stage, and at the end of a season, which was the best time for evaluation because some of the clonal traits develop at the later stages. For clonal organ evaluation, two to ten individual plants of...
each species were excavated with below-ground organs. For
conformity whether we are in correct identification of the
clonal growth organs and life form for each species from
the wetland species pool, we used the CLO-PLA 3 (CLOnal
PLAnts, version 3) of the CLOPLA database (http://clopla.
butbn.cas.cz/). This online data-base of clonal growth of
plants, contains clonal traits and vegetative regeneration
of about 186,157 records of 2923 species for the European
temperate flora. This data-base is freely available and can
serve as a guide for clonal trait sampling in different parts
of the globe, together with specific detailed information on
how to use it and the nature of clonal traits (Klimeš and
Klimešová 1999; Klimešová et al. 2011) and PLADIAS
(Plant Diversity Analysis and Synthesis, 2014–2018) of the
Pladias database of the Czech Flora and Vegetation (www.
pladias.cz) of clonal growth in plants. It includes more than
13 million records of almost 5000 taxa (species, subspe-
cies, varieties and hybrids), which came from seven regional
projects, five large national databases and records collected
within the PLADIAS project. The Pladias database covers
largest set of data on vascular plants of the Czech Republic
(Wild et al. 2019).

Hemicryptophytes are plants whose clonal organs (e.g.,
perennating buds) are at ground level, the aerial shoots
dying down at the onset of unfavorable conditions. Geo-
phytes are perennial plants that possess and propagates by
means of buds, bulbs, tubers, corms, or rhizomes below the
soil surface. Therophytes are plants that pass the unfavora-
ble season only through the seeds but proliferate through
clonal organs like the ramets or clonal offshoots in the
growing season.

The present study covered almost all the major aquatic
habitats, including eight lakes (Anchar, Dal, Wular, Mansbal, Ahansar, Narangbagh, Nilnag and Waskar), five
wetlands (Shallabugh, Tulmula, Hokarsar, Malangpora
and Kranchu), seven streams (Achabal, Bal-Kol, Irriga-
tion canal and spring stream of Sundoo, Nambal rivu-
let, Nagrad stream, Aarpath rivulet and Spring stream)
and two rivers (Jhelum and Sindh) and their tributaries
(Table 1).

River Jhelum is the main river of the Kashmir valley. The
major tributaries of the Jhelum River include: Sind (Gan-
derbal/ Srinag), Lidder (Anantnag), Rambiara (Pulwama/
Kulgam) and Pohru (Kupwara). The minor tributaries of
the Jhelum include, ArapatKol, Vishav, Sandran, Bringi,
and Romushali (Anantnag, Kulgam); Arapal (Pulwama);
Harwan (Srinagar); Rambiara (Shopian); Vij-Dakil, Erin,
Madumati, and Ningal (Bandipora, Bramulla) and Sukhnag-
Firozepora, Dughganga-Shaliganga, (Budgam, Baramulla).
In addition to these, there are many ponds, marshes and
irrigation channels which support various species of aquatic
plants.

Data on origin (geographic origins), degree of invasive-
ness, growth form, life form and stage of invasion of 102
invasive alien plant species in Kashmir Himalaya were
obtained from personal field surveys and other published
sources (Shah and Reshi 2014; Wani et al. 2018) (Onoine
Appendix I) and the majority (72.89%) of invasive alien spe-
cies are of European origin (Fig. 4).

Table 1 Collection sites spread across lakes, wetlands, rivers and
streams with their coordinates

| Waterbody        | Latitude | Longitude | Altitude |
|------------------|----------|-----------|----------|
| Ahansar Lake     | 34.22889 | 74.661389 | 1583     |
| Anchar Lake      | 34.572778| 74.791667 | 1584     |
| Dal Lake         | 34.131944| 74.855833 | 1584     |
| Mansbal Lake     | 34.247778| 74.668611 | 1583     |
| Nilnag Lake      | 33.856111| 74.693333 | 2180     |
| Narangbagh Lake  | 34.980278| 74.855278 | 1587     |
| Waksar Lake      | 34.218333| 74.661111 | 1590     |
| Wular Lake       | 34.335556| 74.548333 | 1580     |
| Hokersar wetland | 34.100556| 74.718889 | 1584     |
| Kranchu wetland  | 33.996944| 74.938611 | 1588     |
| Malangpora wetland| 33.899444| 74.981944 | 1600     |
| Shallabugh wetland| 34.153333| 74.737222 | 1580     |
| Tulmula wetland  | 34.211389| 74.730833 | 1610     |
| Jhelum River     | 33.200556| 74.600556 | **       |
| Sindh River      | 34.184167| 74.667222 | **       |
| Achabal          | 34.717222| 75.217222 | 1662     |
| Bal-Kol (Tangmarg)| 34.050556| 75.417222 | 2010     |
| Stream of Sundoo | 34.683889| 75.183889 | 1661     |
| Nambal rivulet   | 34.667500| 75.167222 | 1660     |
| Nagrad stream    | 34.684167| 75.183889 | 1661     |
| Aarpath rivulet  | 34.685166| 75.167222 | 1660     |
| Spring stream    | 34.667500| 75.167222 | 1661     |
| Shalimar         | 34.834167| 74.500556 | 1583     |
| Ganderbal        | 34.134167| 74.450556 | 1572     |

** represents missing data

Data analysis

Data analysis was done in R Studio (version 1.2.1335; R ver-
sion 3.6.2). To discern the clonality and the invasion stage,
correlation analysis was performed using the RHmisc pro-
gram. Additionally, we attempted to consolidate the individual
contribution of different clonal growth organs toward clonality
and how closely associated the latter is to different life forms
by performing principal component analysis (PCA) using the
ggbiplot package in R studio (Team 2016). Given the avail-
ability of large number of interrelated variables (clonal growth
organs), principal component analysis, with intentions to
reduce the dimensionality of the variables was performed. This
transformed a large number of possibly correlated variables
into an even smaller number of uncorrelated variables called
principal components which are orthogonal (non-correlated)
and arranged in decreasing order of variance.

Results

Clonal growth organs, invasion stage and growth
form categorization

All the clonal species belonging to the various wetlands
and water bodies were categorized into 12 different types
based on the type of clonal growth organs, distributed
among five invasion stages (Table 2) and four different
life forms (Table 3). Most of the species were found to
have more than one type of clonal growth organ and were
hence represented in different clonal growth organ catego-
ries. Clonal plants constituted more than three-quarters
(84.31%) of the investigated 102 alien aquatic species,
with hydrophytes representing 48.8% of all the clonal
species, followed by Hemicryptophytes, Geophytes and
Therophytes with their respective shares to clonality as
26.74%, 16.26% and 8.14%, respectively. To investigate
the contribution of different clonal growth organs toward
invasiveness, presence and absence of eleven variables
(rhizome, stolon, tillers, tubers, turions, runner, buds,
corms, ramets, pleiocorm, fragments) were recorded in
102 species. As shown in Fig. 1, a bimodal distribution
was observed for turions, tubers and stolon. Normal dis-
tributions without any significant skewness were observed
for some others traits.

Clonality and clonal growth organs vis-à-vis stages
of invasion

With the increasing stage of invasion, there is a progressive
increase in the abundance of clonal plants. Out of 34 plant
species at invasion stage V, 31 (91.17%) turned out to be
clonal. The stage V species (most invasive plants) therefore,
represents a maximum fraction of clonal plants (Table 4).

Identification of possible factors (clonal growth
organs) affecting clonality

Clonality in plant species arises due to a number of clonal
growth organs, and some plant species bear more than one
type of clonal organ. To evaluate the relationships between
variables, correlation analysis has been performed in 102
invasive alien plant species. As shown in Table 5, a highly
significant positive correlation has been detected between
clonality and rhizome ($r = 0.993; p < 0.001$) and between
bulbs, corms and pleiocorms ($r = 1; p < 0.001$). Furthermore, highly significant positive correlations were identified between clonality and turions ($r = 0.969; p < 0.001$) and runners ($r = 0.975; p < 0.001$). Also, highly significant positive correlations were identified between rhizomes and turions ($r = 0.985; p < 0.01$) and between rhizome and runner ($r = 0.976; p < 0.01$).

Given the availability of large number of interrelated variables (clonal growth organs), principal component analysis, with intentions to reduce the dimensionality of the variables was performed.

The Eigenvalues that arose out of the principal component analysis show that the first two principal components accounted for 87.2% of the total variance (PC1 52.3%; PC2 34.9%). The percentage of the explained variances surges up to 95.8% when third principal component was taken into consideration (Supplementary Table 6). In view of the large
number (12) of variables studied, PC1 and PC2 were taken for further analysis.

The scores of five invasion stages and the loadings of 12 clonal growth organ variables are shown in Fig. 2. In the PC1, which explains 52.3% of the total variance, there are strong positive loadings for rhizome, turion, runner, clonality, buds, fragments, and tubers. The positive contribution of these variables, particularly fragments, buds, and tubers, to this component indicates their significant contribution toward clonality of species resident at the invasion stage V (Supplementary Table 6, Fig. 2). Again, in the PC1, stolons, pleiocorms, corms and bulbs with moderate loadings seem to contribute considerably to the clonality of species resident at invasion stage III. Similarly, PC2, which makes out 34.9% of the total variability in the data, depicts strong positive loadings for ramets, buds, turions, tubers, tillers and fragments. Among all these clonal growth organs, though with moderate loadings tillers are found to contribute significantly to the clonality of species placed at invasion stages IVa, IVb, and II. (Fig. 2, Supplementary Table 6).
Clonality, life forms and clonal growth organs (CGO’s)

The alien aquatic plant species distributed among four different life-form categories having 12 types of clonal growth organs with some species showing more than one type of clonal organs. PCA was done to analyze the association between clonality, life form and different types of clonal growth organs. Figure 3, Supplementary Table 7 provide the outcome of PCA. 86.6% of the total variance in the data set is attributed to the first two principal components with respective shares of 65.6% and 21%. With the inclusion of the third principal component (PC3), 100% of variance in the data set gets explained (Supplementary Table 7).

The PC 1, which accounts for 65.6% to the total variance in the data set shows strong positive loading for ramets, corms, tillers, bulbs, and pleiocorms. The PC2, which adds 21% to the total variance, exhibited strong positive loadings for tubers, turions, and fragments. The same directionality of these strongly contributing factors and clonality alongside other low contributing factors like stolons, rhizomes, runners, and buds point to the close association of clonality and all these factors (Fig. 3, Supplementary Table 7). A keen look at Fig. 3 also indicates that a major share of fragments, turions, runners, rhizomes, stolons and buds contribute strongly to the clonality of hydrophytes. Tubers and ramets as seen in the biplot seem to contribute to the clonality of geophytes. Besides imparting to the clonality of geophytes ramets also appears to add to the clonality of therophytes in association with tillers, corms, pleiocorms, and bulbs. Finally, pleiocorms and bulbs besides sharing to the clonality of therophytes, also add to the clonality of hemicryptophytes.

Discussion

Arbitrarily linking species invasiveness to clonality without figuring out the principal components seems rather unrealistic and has greatly redacted the highly useful information on invasive species. Since, in our case, 84% of the studied...
species and almost 90% of the most invasive species (stage V) turned out clonal, it is quite rational to discuss future implications of the clonality on species invasions and range shifts. A highly significant positive correlation found between clonality and invasiveness substantiates this association at a reasonably wide regional scale, representing the entire Kashmir Himalayan region. The distinction of clonal growth forms and significant positive correlation between clonality and different clonal growth organs (rhizomes, runners and turions), further affirms the strong nexus of clonality with species invasions (see Fig. 4).

These results, though in concordance with some recent studies (Liu et al. 2006; Shah and Reshi 2014), are credited to unveil new grounds behind successful spread of clonal species in wetlands. We ascribed this mainly to the novel analytical approach and a more comprehensive study region than the previous studies. Earlier, Reichard and Hamilton (1997) reported a close correlation between the invasiveness and clonality of American wetland plants. Since the association of clonality and invasiveness is thought to be species-specific (Liu et al. 2006), studies like those of Pyšek et al. (2002), advocating production of invasive hybrid genotypes by rare sexual reproduction and their clonal growth-mediated fixation benefits over native species (Liu et al. 2006), are highly recommended. Our work stands distinct from those done in the past (e.g., Reichard and Hamilton 1997; Maurer and Zedler 2002; Liu et al. 2006; Shah et al. 2014b) mainly because of inclusion of more study sites and dimensionality reduction in the data set, affording least loss of original information. There are a considerable number of invasive plant species that are capable of vigorous clonal propagation, and their invasiveness may be related to clonal integration (Liu et al. 2006). Many studies have shown that clonal integration can enhance plant invasion success in alien plants (Reichard and Hamilton 1997; Liu et al. 2007; Aguilera et al. 2010; Roiloa et al. 2010; Roiloa et al. 2010). Other pieces of evidence in favor of the clonality–invasiveness correlation which strongly corroborates our findings are that of Chittka and Schürkens (2001) and Minghua and Ming (2002), suggesting that most serious invaders are better adapted to environmental conditions (Hutchings and de Kroon 1994; Ming 1996a; Song et al. 2002), and displace natives through intense competition. Although varied and many, the prime and worthwhile advantages of having CGOs in heterogeneous habitats include reduction of genetic risk (Cook 1985; Ming 1996b), efficient sharing of resources within a clone (Peltzer 2002), foraging behavior (Hutchings and de Kroon 1994) and proper apportionment of labor (Alpert and Stuefer 1997). In comparison to terrestrial habitats, aquatic systems have been found to accommodate a greater fraction of invasive species with a disproportionate representation of clonal (Wani et al. 2018). High vegetative multiplication concurrent to efficient nutrient use and vigorous growth (Pyšek and Richardson 2008) grants competitive advantage and invasive potential to exotic invaders in non-native ranges.

Several studies have shown that residence time is a significant determinant of invasiveness and there is strong correlation between invasion stage or species invasiveness with the time of introduction (Wilson et al. 2012; Pyšek and Jaroslík 2005; Blossey et al. 2021). However, in our study, we found many species that were introduced or reported very recently in Kashmir Himalaya but have occupied advanced stages of invasion due to their fast spread. For example, species like Hydrocharis morsus-ranae, which was reported in 2016 in Kashmir Himalayan wetlands and has occupied IVb invasion stage (Ganaie et al. 2016). Similarly, other species like Azolla cristata and Nymphaea alba reported in 2012 and 2020 are at invasion stages V and IVb, respectively (Ahad et al. 2012; Hassan and Nawchoo 2020). Based on the above information, it seems that invasiveness is not influenced only by the time of introduction, but many other factors like life-history traits, socioeconomic factors, and environmental variables, also affect the spatial distribution of invasive species (Thuiller et al. 2006). Similarly, many studies have shown that many factors, such as species life form and strategy, early flowering, tall stature, sexual reproduction, ploidy levels, and opportunistic dispersal, by a number of vectors are the key determinants of species invasiveness (Pyšek et al. 2009; Dar et al. 2020).

In addition, clonal growth organs enable plant species to exploit vacant resource-abundant patches, and the interconnected networks of ramets in some cases are believed to mediate in transfer of information and resources, besides their storage (Latzel and Klimešová 2010; Klimešová et al. 2011; Song et al. 2013; Cornelissen et al. 2014). Enhanced anchorage and formation of dense canopy by clonal macrophytes in wetlands also reduce the effects of different aero- and hydrodynamic forces (Sand-Jensen and Mebus 1996; Liu et al. 2007). Furthermore, lateral expansion of clonal plants in stressful conditions of running water successfully economizes resource utilization at the cost of less-efficient non-clonal plants (Ganie et al. 2008). Diversity in clonal architecture of plants may enhance their performance under varied environmental conditions (Gray 1986; Dehler 2003; Richards et al. 2006; Richardson and Pyšek 2006; Funk 2008), allowing these species to invade a wide range of habitats. Notwithstanding the multitude of benefits by being clonal, the associated dispersal limitations slow down the invasion pace (Pyšek 1997), which in most cases is offset by having both sexual and asexual reproductive means with plastic allocation to each reproductive strategy (Eckert 2002).

Uniparental reproduction (e.g., asexual reproduction) during colonization can provide reproductive hedge when mating partners are sporadic (Eckert et al. 2006). However,
asexual reproduction hampers opportunities for genetic admixture and recombination, which can expand founder effects and upturn the probability of stochastic processes prompting patterns of genetic polymorphism (Husband and Barrett 1991; Kliber and Eckert 2005). Furthermore, the prolific clonal dispersal of vegetative propagules can promote “mate finding”, mostly in aquatic plants (Barrett 2015). In species in which clonal propagation preponderates, mutations decreasing fertility may lead to sexual dysfunction and even the loss of sex. Recent evidence suggests that somatic mutations can play an important role in prompting fitness in clonal plants and may also help to determine the genetic variability in sterile clonal populations (Ally et al. 2010; Bobiwash et al. 2013). Clonal aquatic plants often persist for longer periods in wetland habitats in which sexual reproduction is prevented, either because of the absence of mating partners, lack of pollinators, or where ecological conditions are unfavorable for seed germination, seed set, or seedling establishment (Barrett 2015). Long-distance dispersal of only one mating type to a region, especially in invasive species, may disable sexual systems, resulting in sterility (Zhang and Shu 2010). Asexual reproduction in clonal plants also provides several evolutionary benefits, including the gain of advantage by avoiding the costs associated with sexual reproduction and a means by which clonal species can be rapidly adapted after colonization to the new environments they face (Barrett 2015).

Higher phenotypic plasticity and a wider range of clonal growth organs in aquatic plants in the form of corms, rhizomes tubers, and turions (Barrett et al. 1993; Grace 1993; Eckert et al. 2016) provide avenues for understanding the evolutionary and adaptive significance of variable resource allocation to growth and reproduction along moisture gradients. Furthermore, raising the life-time reproductive success and guaranteeing the future population establishment prospectus in aquatic plants via persistent genets require some trade-offs particularly priority of asexual over sexual reproduction (Eckert et al. 2016). Many reports suggest that clonal plants allocate more resources to vegetative than sexual reproduction under subdued light conditions in water to increase their future persistence (Li et al. 2019). There are also concrete evidences suggesting clonally propagated plants to be more successful in aquatic habitats which face frequent ecosystem disturbances and follow-up recoveries (Eckert et al. 2016; Zhang et al. 2019).

Conclusion

Our results showed strong association of clonal architecture with not only the stages of invasion, but also the distribution pattern of alien species in aquatic habitats, thereby indicating the pivotal contribution of clonality in invasions. The distinction of clonal growth forms and significant positive correlation between clonality and different clonal growth organs (rhizomes, runners and turions), further affirms the strong nexus of clonality with species invasions. Future studies directed at unraveling the mechanistic reasons behind clonality should include genomics of the concerning species in the models in an evolutionary context to better inform the management models for aquatic plant invaders.

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Availability of data and materials All data generated or analyzed during this study are included in this published article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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Conclusion

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