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The Influence of Geographical Factors on Polyploidy in Angiosperms with Cartographic Evidence from the Northwestern Himalayas: A Review

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ABSTRACT

The review paper comprised the impact of geographical and environmental factors on polyploidy and vice versa. The review covers different effects of geographical factors, like spatial isolation, altitude, and local climate on polyploidy, and the behavior of polyploid(s) in abiotic factors, such as temperature and light with a few examples of northwest Himalayas. The paper concludes that polyploid plants behave differently in environmental conditions, as polyploids are more prominent in higher altitudes, colder environments, and nutrient-rich soil than diploid progenitors, but have a mixed distribution in different geographical conditions. Further, polyploidy is more common among perennials than annuals, while niche differentiation depends more on the local environment. The virtual case study results from North and North Western India have been shown with the help of ArcGIS online software. The scrutiny of spatial distribution on maps highlights the fact that polyploidy is still a complex research puzzle with interesting perspectives.

INTRODUCTION

Polyploidy or whole genome duplication (WGD), a naturally occurring phenomenon in plants (rare in animals), involves more than two whole sets of chromosomes and is considered a key determinant in studying plant evolution. This inducible phenomenon results in multiple gene copies, which led to genome plasticity and adaption by the neo-fictionalization of genes (Cheng et al. 2018). Polyploidy can arise naturally in many ways, either by chromosome doubling in meristematic cells during mitosis or by the fusion of unreduced gametes in meiosis (Lewis 1980, Levin 2002, Ramsey & Ramsey 2014). In nature, polyploids are of three types: autopolyploids, allopolyploids, and segmental allopolyploids (Stebbins 1947). The effect of chromosomal duplications on phenotypes has attracted the attention of researchers since the beginning of the 20th century (Stebbins 1947) and is well known as the "gigas effect," i.e., enlargement of cellular size in both flora and fauna (Stebbins 1971, Knight & Beaulieu 2008). It is evident in plants that polyploidy modifies physiological features like transpiration, photosynthesis, and growth rates (Otto & Whitton 2000, Levin 2003, Maherali et al. 2009, Pacey et al. 2020, Van De Peer et al. 2021), which further improves its ecological tolerance (Levin 2002). Polyploids also have increased reproductive efficiency, are known to have more flowers per inflorescence, and reduce the barrier of self-incompatibility (Robertson et al. 2010). The polyploids are often thought to be ecologically better adapted and show gigas effect over diploid progenitors (Stebbins 1971). Such effects might be a result of increasing genome size (DNA), which relatively increases the level of gene and protein expression, and also increases the cell size, reduces cell division, and delays the onset of flowering and reproductive growth (Stebbins 1971). Hence, the insight of all the above characters and the molecular studies of over a decade show that polyploids are better adapted than their diploid ancestors (Otto & Whitton 2000, Comai 2005), and may help in species diversification in the harsh ecological environment (Otto 2007), where polyploid species evolve much faster or in a different direction compared to the diploids (Otto &Whitton 2000). The current review emphasizes the impact of abiotic factors, such as soil, temperature, light, and other geographical factors on polyploidy. The detailed review has been presented for the entire globe with special reference to the studies conducted by different scholars in northwest India (Table 1).

INCIDENCE OF GEOGRAPHICAL FACTORS OF POLYPLOIDY

Geographical Isolation

The spatial distribution of sexual asexual taxa is termed "Geographical parthenogenesis". Later on, many authors discussed the broader geographical distribution of asexual(s). It is a belief that polyploidy enhances the adaptability of apomictic plants in higher elevations (Bierzychudek 1985) or extreme range of niches (Vrijenhoek 1984), but, very little is known about the vegetative performance and reproductive fitness of plants in severe alpine conditions (Ladinig et al. 2013). Parapatric distribution of the *Centaurea phrygia* (2x and 4x) was reported in Central Europe (Koutecký 2012), and of these, diploids are prominently distributed all over Central and North Europe, while tetraploids are confined to Western Carpathians. Similar observations were also observed in the *Centaurea* sect. Jacea, where a diploid/tetraploid paring, leads to a low incidence of triploid(s) in both natural/experimental populations (Hardy et al. 2000, 2001, Koutecký et al. 2011). Triploids have reported being sterile or nearly so, in the population of the *Centaurea* sect. Jacea (Hardy et al. 2000, 2001). The distribution of cytotypes (parapatric) depends upon two mechanisms: minority cytotype exclusions or habitat differentiation (Hardy et al. 2000). The study on habitat requirement in cytotype(s) has been documented in both natural and laboratory conditions (Van Dijk et al. 1992). However, the distribution of polyploidy is not directly related to geographical isolation, as there are few reports of sympatric speciation, viz. *Aster thomosonii* and *Elsholtzia cilliata* (Fig. 1, Table 1).

Altitude Variation

It is believed that polyploidy predominance increases with an increase in altitude and are adapted more to cold temperature than diploid ancestor (Hagerup1932). Löve and Löve (1957) observed similar results in the higher altitudes of Eurasia and Arctic regions, where 85.9 percent polyploids were recorded compared to lower altitude flora (37%), and a similar view was supported by many scholars (de Wet 1980, Soltis & Soltis 1999, Brochmann et al. 2004). However, the theory of better resilience of polyploids was firmly rejected by many scholars (Bowden 1940, Gustafsson 1948). It is generally

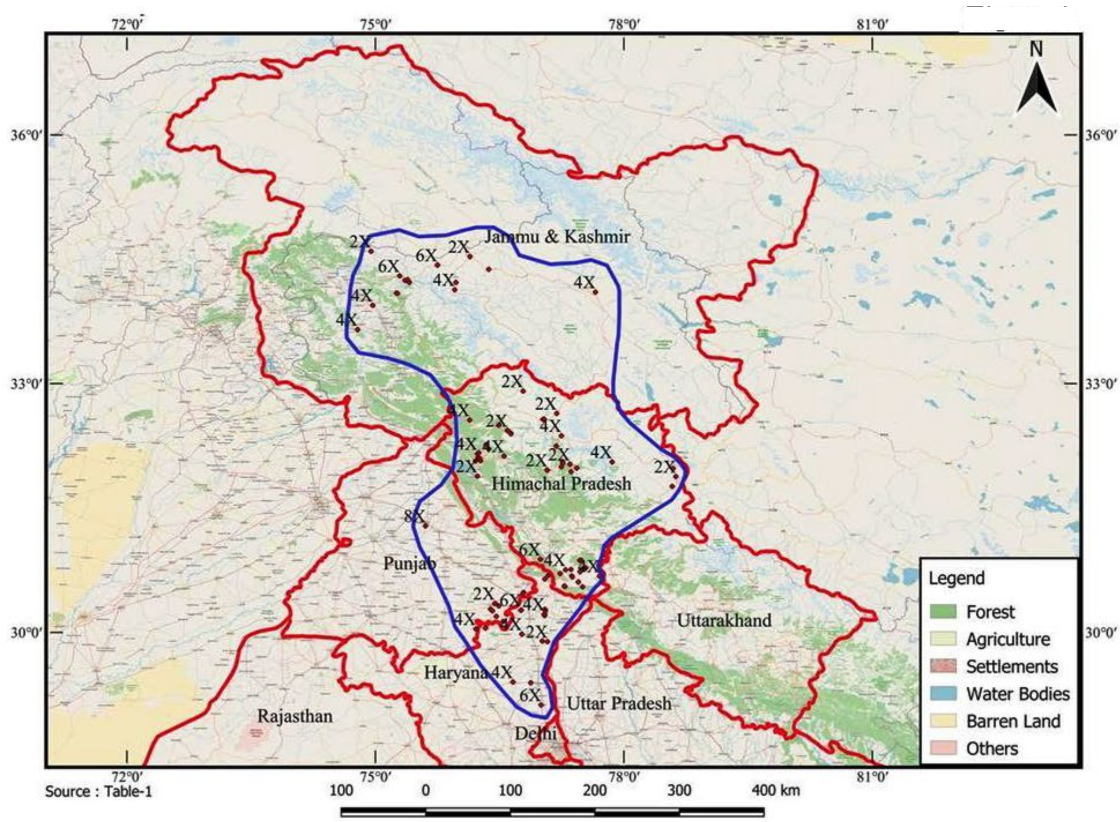

Fig. 1: Incidence of polyploidy and land use pattern in North and North Western India.

Table 1: List of Intraspecific cytotypes reported in Northwest Himalayas.

S. No.	Name of Taxon	Diploids	Polyploids					References
		2x	3x	4x	6x	8x		
1.	*Agrimonia eupatoria* L. (x=7)	Dharmshala, (H.P) (PID: 102001) Kangra, (H.P) (PID: 102002) Timbi, Sirmaur (PID: 102003)		Palampur (H.P.) (PID: 104002) Kangra (H.P.) (PID: 104003) ChurDhar, Simraur (PID: 104004) Aharbal, Kashmir (PID: 104006)	Sonmarg; Kash-mir (PID: 106001)			Kumar et al. (2011a)
2.	*Ajuga parviflora* Benth. (x=16)	Sangrah, Sirmaur (PID:102005)		Haripurdhar, Sirmaur (PID: 104021)				Singh et al. (2018b)
3.	*Alchemilla vulgaris* L. (x=17)	Aru, Kashmir (PID: 102004)					Thajwas, Kashmir (PID: 112001)	Jeelani et al. (2012)
4.	*Argimon emexicana* L. (x=7)	Dehra, Kangra (H.P.) (PID: 102006)		Kalaamb, Sirmaur(H.P.) (PID: 104022)				Jeelani et al. (2014)
5.	*Artemisia martima* L. (x=9)	Manali (H.P.) (PID: 102007)						Gupta et al. (2014a)
6.	*Artemisia scoparia*Waldst. ex Kit. (x=9)	Manikaran Sahib (PID: 102008)		Baru Sahib, Sirmaur (PID: 104007)				Gupta et al. (2014a)
7.	*Aster thomsonii* L. (x=9)	Shilai, Sirmaur (PID: 102009)		Churdhar, Sirmaur (PID: 104008)				Gupta and Singh 2015
8.	*Brachyactis pubescens* (DC.) Aitch. & C.B.Clarke (x=9)	Drass, Leh and Ladhakh (PID: 102010)		Schnag, Leh and Ladhakh (PID: 104009)				Tantray et al. (2018)
9.	*Cenchrusciliaris*L. (x=12)			Mullana, Ambala (PID: 204001)	Jabli, Shivaliks			Dhaliwal et al. (2018a)
10.	*Cynodon dactylon* (L.) Pers. (x=9)	Barara, Ambala (PID: 202001)		Pinjaur, Panchkula (PID: 204002)				Dhaliwal et al. (2018b)
11.	*Dicanthium annulatum* (Forssk.) Stapf (x=10)	Indri, Karnal (PID: 202002)		Lalru, Ambala (PID: 204003)				Gupta et al. (2017b)
12.	*Digitaria ciliaris* (Retz.) Koel. (x=9)			Barara, Ambala (PID: 204004)	Mohri, Ambala (PID: 206002)	Mirpur, Rewari (PID: 206002)		Gupta et al. (2017a)
13.	*Elsholtzia ciliate* Benth. (x=8)	Thajwas, Kashmir (PID: 102011)		Thajwas, Kashmir (PID: 104010)				Malik et al. (2012)
14.	*Geranium pratense* L. (x=14)	Mulbekh (PID: 102012)		Drass (PID: 104011)				Khan et al. (2020)

S. No.	Name of Taxon	Diploids		Polyploids			References
		2x	3x	4x	6x	8x	
15.	*Hemarthria compressa* (L.f.) R. Br (x=)	18 Sriganganagar (PID:)		36 Indri, Karnal (PID: 204005)			Gupta et al. (2017b)
16.	*Hieracium umbellatum* (x=5, 9)	Jispa, Spiti (H.P.), (PID: 102014)			Keylong, Lahaul (H.P.), (PID: 106002)		Gupta et al. (2014b)
17.	*Imperata cylindrica* (L.) P. Beauv. (x=10)	Mullana, Ambala (PID: 202004)		Morni, Panchkula (PID: 204006)			Gupta et al. (2017b)
18.	*Inula grandiflora* (x=8)	Nerang, Kullu (PID: 102013)		Malana, Kullu (PID: 104012)			Himshikha et al. (2017), Gupta et al. (2017a)
19.	*Panicum antidotale* Retz (x=9)	Cheeka, Kithal (PID: 202005)		Safidon, Jind (PID: 204007)			Bir and Sahni (1985)
20.	*Papaver dubium* L. (x=7)	NahanSirmaur (H.P.) (PID: 102015)		Ratnipora, Pulwama (PID: 104013)			Kumar et al. 2013
21.	*Pennisetum purpureum* (x=7)			Khaniara, Kangra (PID: 104014)	Loharari, Kangra (PID: 106003)		Kaur et al. (2014)
22.	*Physochlain apraealta* (Decne.) Miers. (x=21)	Nako Lake (PID: 102016)		Panikhar Village (PID: 104015)			Singhal et al. (2017)
23.	*Plantago depressa* Willd. (x=6)	Nahan, Sirmaur (PID: 102017)		Sangrah, Sirmaur (PID: 104016)	Chapdhar, Sirmaur (PID: 106004)		Gupta et al. (2017c)
24.	*Primula denticulata* Sm. (x=11)	Sanko, Ladhakh (PID: 102018)		Dundi village,Kullu (PID: 104017)			Singhal et al. (2018)
25.	*Ranunculus hirtellus* Royle (x=8)	GauriKund, Chamba (PID: 102019) Manimahesh hills, Chamba (PID: 102019)		Rohtang Pass, Kullu, (PID: 104018) Keylong, Lahaul-Spiti (PID: 104019)			Kumar andSinghal (2011)
26.	*Rorippa palustris* (x=7)	Suru Valley (PID: 102021)			Drass Valley (PID: 106005)		Khan et al. (2019)
27.	*Saccharum bengahlense* (x=10)	Patiala (PID: 202006)		Patiala (PID: 204008)	Patiala (PID: 206001)		Bir et al. (1992)
28.	*Saxifraga diversifolia* (x=4, 5)	Thajwas, Kashmir (PID: 102022)		Barabhnagal, Kangra (PID: 104020)			Kumar et al. (2011b)
29.	*Scirpus roylei* (Nees) R.Parker(x=11)	Patiala (PID: 202007)				Jalandhar (PID: 208001)	Dhaliwal et al. (2018b)
30.	*Setaria glauca* (L.) P. Beauv.(x=9)			Barara, Ambala, (PID: 204012)		Lalru, Ambala (PID: 208002)	Gupta et al. (2018)
31.	*Setaria verticillata* (L.) P. Beauv. (x=9)	Mirpur, Rewari (PID: 202011)			Ganaur, Sonipat (PID: 206003)		Bir and Sahni (1985) Gupta et al. (2018b)

S. No.	Name of Taxon	Diploids	Polyploids				References
		2x	3x	4x	6x	8x	
32.	*Sibbaldia micropetala* (x=7)	Churdhar, Sirmaur (PID: 102023)		Shilai, Simaur (PID: 104023)			Kumar et al. (2012)
33.	*Siegesbeckia orientalis* L. (x=15)	Sangrah, Sirmaur (PID: 102026)		Chapdhar, Sirmaur (PID: 104025)			Singh et al. (2018a)
34.	*Silene vulgaris* (Moench) Garcke (x=12)	Udaipur, Lahaul-Spiti (PID: 1020244) Dhancho, Chamba (PID: 102025)		Malana Village, Kullu (PID: 104024)			Gupta et al. (2018a)
35.	*Sium latijugam* C. B. Clarke' (x=12)	Gurez, (PID: 102027)		Aru, (PID: 104026)			Jeelani et al. (2012)
36.	*Spergularia diandra* (Guss.) Heldr. &Sart. (x=9)	Pooh, Kinnaur (PID: 102028)		Chango, Kinnaur (PID: 104027)			Kaur & Singhal (2011)
37.	*Sporobolus diander* (Retz.) P. Beauv.(x=9)	Sanauli, Panipat (PID: 202008)		KUK, Kurukshetra (PID: 204009)			Dhaliwal et al. (2018b)
38.	*Sporobolus helvolus* (Trin.) T. Durand and Schinz. (x=9)	Lalru, Ambala (PID: 202009)		Ferozpur			Dhaliwal et al. (2018b)
39.	*Sporobolus marginatus* Hochst. ex A. Rich (x=9)	Sadhu Vela, Punjab (PID: 202010)		NIS, Patiala (PID: 204011)			Dhaliwal et al. (2018b)
40.	*Strobilanthes alatus* Nees. (x=8)	Haripurdhar, Sirmaur (PID: 102029)		Chapdhar, Sirmaur (PID: 104028)			Singh et al. (2016)
41.	*Taraxa cumofficinale* (x=8)	Jari, Kullu (PID: 102030)	Malana, Kullu (PID: 103001)	Nerang, Kullu (PID: 104029)			Gupta et al. (2017a)
42.	*Thalictrum foliolosum* (x=7)	Sali, Kangra, H.P. (PID: 102032)		ChottaBhangal, Kangra, H.P. (PID: 104030)	Jabli, Shivaliks (PID: 106006)		Rani et al. (2014)
43.	*Tordyliopsis brunonis* DC. (x=11)	BhaironGhat (PID: 102033)	Manimahesh (PID: 103002)				Kumar et al. (2014)
44.	*Tragopogon dubius* Scop. (x=7)	Keylong, (H.P) (PID: 102034)		Lossar, Spiti (H.P.) (PID: 104031)			Gupta et al. (2014b)
45.	*Urochloa panicoides* (x=8)	Sadhubella, Patiala (PID: 202012)		Bahadurgarh, Patiala (PID: 204013)	Mohri, Ambala, (PID: 206004)		Bir et al. (1988)
46.	*Valeriana jatamansi* (x=8)	Salooni, Chamba (PID: 102035)		Tisa, Chamba (PID: 104001)		Kullu (PID: 108001)	Rani et al. (2015)
47.	*Verbena officinalis* L (x=7).	Sangrah, Sirmaur (PID: 102036)				Sangrah, Sirmaur (PID: 108002)	Singh (2017)

*PID- , x-basic chromosome number

believed that plants reproducing asexually frequently grow on higher altitudes and latitudes than their sexual relatives (Bierzychudek 1985, Hörandl et al. 2008) and most of these are polyploids. Fig. 2 indicates that the spatial patterns of polyploidy have no direct relation with altitude in the reviewed sites of the northwestern Himalayas.

Polyploidy and Temperature

Cytogeographical studies reveal polyploids replace diploid ancestors along with ecological gradients since polyploids generally prefer drier habitats (Watanabe 1986, Maherali et al. 2009) and extensively exposed habitats (Watanabe 1986, Lumaret et al. 1987). However, Fukuda (1967) reported the opposite of this, where diploid species of *Achlys* are dominant over tetraploids. As an earlier view, polyploidy is higher in plants of cold temperatures (Hieter & Griffith 1999). It is believed that cold stress alters the microtubule formation, which obstructs cytokinesis and ultimately, forms unreduced gametes (Ramsey & Schemske 1998, Bomblies et al. 2015), which is a potent cause of sexual polyploidization (De Storme et al. 2012). This view is experimentally supported by Otto and Whitton (2000) that the frequency of unreduced gametes can be increased with cold temperature treatments. However, in northern latitudes, the high ploidy level in the species is due to the dominant perennial life forms and is not related to the lower temperature adaptability (Soltis et al. 2004). The more frequency of polyploids at high altitudes, the more ecological adaptation and efficiency than diploid ancestors (Vamosi & Dickinson 2006). It is evident that in higher altitudinal ranges, most plant species adapt to perennial life forms, and annuals are mostly dominant in lower altitudes. In the end, the perennial polyploids are more adaptive to a colder temperature than diploid progenitor and annuals cohorts, which has been also observed in the northwest Himalayas.

Polyploidy and Habit Correlations

According to de Wet (1980), the origin and ecological adaptation of polyploids depend upon habit, habitat, and breeding system, which makes the relationship between polyploidy and habit more critical. Polyploidy usually occurs in perennial herbs than annuals and woody species (Stebbins 1950, 1971). Perennial life form, despite lack of immediate fitness, provides a better chance for autopolyploids and allopolyploids to conquer the sterility problems that arise due to chromosome pairing and interaction between new cytoplasmic genomes (Hilu 1993). Generally, polyploids have the advantage of additional alleles that increase biochemical and genic flexibility, and heterozygosity, which provides a broader range of habitat adaptability in harsh

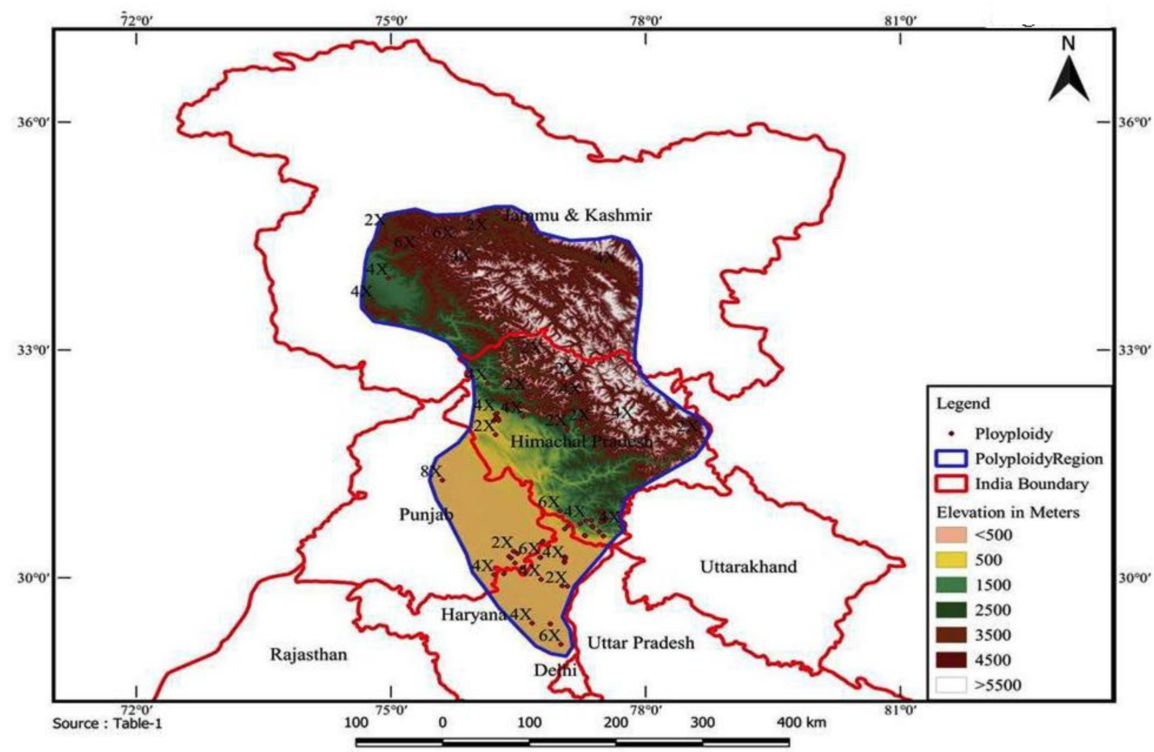

Fig. 2: Altitude variation and predominance of polyploidy in North and North Western India.

and unstable climates over diploid progenitors (Stebbins 1985, Matzke et al. 1999). However, all the polyploids are not only perennials, numerous annuals polyploids are equally successful. The broad-scale comparative studies also highlight that polyploidy is similarly widespread in annuals and perennials with diverse life histories and ecological characters (Vamosi & Dickinson 2006). Otto & Whitton (2000) reported polyploidy index (PI) in ferns (41.7%), monocots (31.7%), and dicots (17.7%), meaning that almost half of the new haploid chromosomes are the result of polyploidization in ferns and so forth. Nevertheless, within dicots, herbaceous dicots have more PI (26.3%) compared to woody (-2.2%), which means a positive correlation is found in herbaceous dicots, while it is missing in the latter (Otto & Whitton 2000). The low polyploidy rate in woody angiosperms and gymnosperms may be due to the constraining cell size of vascular cambium, and ecological/historical factors like a reduced rate of new habitat emergence (Stebbins 1971). Further, chromosome conditions of the phanerogams correspond to life forms as annuals generally show low base numbers and keep to the diploid or other lower polyploidy, while perennials, attain high base numbers and ploidy level (Gustafsson 1948). As per previous studies, in Pakistan only, two different views are reported for polyploidy and perenniality, polyploidy is rich in perennials in the first view (Baquar 1976), while it is more in annuals (Khatoon & Ali 2006) in another view. While in Polish flora, perennials and woody plants generally had higher chromosome numbers and polyploid frequencies than annuals and biennials (Góralski et al. 2014). However, due to some antagonistic reports (Vamosi & Dickinson 2006), no direct conclusion can be drawn for the correlation between polyploidy and herbaceous growth habit. Although, there is a shift from annual habit to perennial in the case of polyploids (Sano et al. 1980), which might be due to increased cell size that provides an advantage of superior longevity and slower metabolism (Garbutt & Bazzaz 1983). The evolutionary analysis of 1751 angiosperms species for polyploidy, clonality, and life history, reveals a significant relationship between polyploidy and perenniality (Van Drunen & Husband 2018a, b).

Polyploidy is among the critical determinants in studying plant evolution and results in genome plasticity and adaption by neo-fictionalization of genes. The current study predicts that environmental factors do not have any direct relation to the geographical/environmental allocation of cytotypes, but can promote chance colonization. Polyploid plants behave differently in other environmental conditions, as polyploids are more prominent in higher altitudes, and colder environments, and have a mixed distribution in different geographical conditions.

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