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Continuing the search for pattern among rare plants: are diploid species more likely to be rare?

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ABSTRACT

Questions: Are diploid plant species more endangered than polyploids? Does ploidy play any role in rarity and invasiveness of plant species?

Data studied: I surveyed and analysed ploidy levels of more than 1000 plant species, including 75 endangered taxa and 43 invasive species, on the Indian subcontinent to test the relationship between ploidy and both rarity and invasiveness.

Search method: *Null hypothesis*: I examined the null hypothesis that diploids and polyploids were equally represented in the sets of endangered and non-endangered/non-invasive species. *Logistic regressions*: I performed simple logistic regressions (logit model) of the probability of species endangerment and invasiveness on number of chromosomes. Where necessary, plant family was included as a co-factor in the regressions, to partially control for the effects of phylogenetic autocorrelation among species.

Conclusions: I show that diploid plant species in the Indian subcontinent are more likely to be rare than are polyploids. The analysis revealed that the diploid–polyploid ratio for non-endangered plants of the subcontinent follows known trends (with 50.5% diploid), but that a significantly larger fraction of the endangered species (64%) are diploid. Clear polyploids comprise only 36% of the endangered species. In contrast, a significantly larger fraction of invasive species studied (72%) are polyploids, with many displaying high levels of polyploidy. The relationship between diploidy and both plant rarity and invasiveness was highly significant. I also find that, in general, plant species with more chromosomes have less likelihood of being endangered than the species with fewer chromosomes. Using a simple logistic regression (logit model), I show that phylogeny has a significant effect on species endangerment and that chromosome number is negatively and significantly correlated to the probability that a species is endangered.

Keywords: diploidy, Indian subcontinent, invasiveness, plant species, polyploidy, rarity.

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INTRODUCTION

Loss of plant and animal species owing to habitat destruction and over-exploitation is an ongoing process. However, the inherent causes of species' proneness to rarity and extinction are still not well understood. Researchers have suggested that several different mechanisms could be responsible for rare–common differences, which may be difficult to differentiate (Kunin and Gaston, 1993). The search for a common pattern in rarity among plants and animals continues albeit with equivocal results. Several studies have noted taxonomic or phylogenetic patterns in rarity (Kubitzki, 1975, 1977; Fiedler, 1986; Hodgson, 1986; Cadotte and Lovett-Doust, 2002). A number of recent studies have demonstrated that vulnerability of birds and mammals to extinction is a function of small taxon size (Purvis and Gittleman, 2000; Purvis *et al.*, 2000), and that taxon size may also be related to rarity in plants (Schwartz and Simberloff, 2001). Several other mechanisms that aim to explain relative abundance and rarity in plants lack uniformity and consistency (Rabinowitz, *et al.*, 1989; Grace and Tilman, 1990; Belsky, 1992; Gaston, 1994; Reader, 1998). However, documenting the properties of rare and common species is important for biological conservation. The search for pattern in rarity must, therefore, continue as it will help us to set priorities for species conservation efforts (Schwartz, 1993). This study focuses on the correlation of ploidy levels/chromosome numbers with rarity and invasiveness as a contribution towards understanding one such mechanism. Specifically, I test the hypothesis that ploidy level/chromosome number is related to the rarity and invasiveness of plant species of the Indian subcontinent.

METHODS

I compiled and analysed data on chromosome number for all the species of 62 randomly selected plant families of the Indian subcontinent for which such data are available. These plant families represent various phylogenetic groupings (primitive and advanced; monocots and dicots), physiognomic types (trees, shrubs, and herbs), and habitat ranges (terrestrial and aquatic). The chromosome counts for 1183 species analysed here were derived from the *Chromosome Atlas of Flowering Plants of the Indian Sub-continent* (Kumar and Subramaniam, 1985). I defined endangered species as those listed as rare, vulnerable, and endangered in the *Red Data Book of Indian Plants* (Nayar and Sastry, 1987–1990), and non-endangered species as those not listed in the same source. Of the 560 listed endangered species of the subcontinent, chromosome numbers are published and known for only 75. The invasive species ($n = 61$) included in this study refer to taxa that are listed as such by the Global Invasive Species Database for India (www.iisg.org/database). Of these invasive species, chromosome numbers are known for 43 species that are included in this study. In the present analysis, I classified 75 species as endangered, 43 species were classified as invasive, and 1065 species as non-endangered and non-invasive. The use of terms such as 'diploidy', 'polyploidy', 'commonness', 'rarity', and 'invasiveness' in this study follows their use in standard published literature. I followed the criterion of mean gametic chromosome number of ≤ 15 to classify a species as diploid (Klekowski and Baker, 1966; Soltis and Soltis, 2000). The plant species with a gametic chromosome number of 16 or more, or showing euploidy, were designated as polyploids. The chromosome numbers of endangered, invasive, and non-endangered/non-invasive species were analysed across different families to determine the ratio of diploids and polyploids among these taxa. In all data sets care was taken not to include chromosome counts of domesticated or cultivated species in which polyploidy is very common. I additionally used the chromosome number as a direct measure of ploidy levels to avoid arbitrary and at times artificial division of species into diploids or polyploids. For the species with multiple records of chromosome number, the median value was calculated and used in the analysis.

I tabulated the respective chromosome numbers of various categories of species and expressed the results as percentage diploids and polyploids for each class. The ratio of diploids to polyploids in non-endangered/non-invasive species was approximately 50 : 50, which follows the trends reported in most surveys of angiosperm ploidy levels (e.g. Stebbins, 1950; Grant, 1981; Soltis and Soltis, 2000). I compared the preponderance of diploids and polyploids among the endangered species with those of the non-endangered species, using a chi-square test to evaluate the null hypothesis that proportions of diploids and polyploids do not differ significantly between the groups. The hypothesis was tested to compare proportional representation of: (1) diploids and polyploids in non-endangered/non-invasive species, (2) diploids and polyploids in endangered versus non-endangered/non-invasive species, and (3) diploids and polyploids in invasive versus non-endangered/non-invasive species. I also performed simple logistic regressions (logit model) of the probability of species endangerment and of species invasiveness as a function of chromosome number. This was done to test the hypothesis that the continuous variable, chromosome number (rather than the dichotomous diploid/polyploid distinction), could be related to the rarity and invasiveness of the plant species. Where necessary, plant family was included as a co-factor in the regressions, to control for the effects of phylogenetic autocorrelation among the species.

RESULTS

I observed a strong and significant relationship of ploidy levels with rarity and invasiveness in plant species of the Indian subcontinent. Table 1 gives the proportion of diploids and polyploids in endangered, invasive, and non-endangered/non-invasive species. In the non-endangered species studied, about 50% are diploids and 48% are clear polyploids, with the remaining species having anueploid records. The analysis shows that diploids and polyploids are equally represented in non-endangered species and their differences from the expected ratio are not significant ($Z = 0.896$; $P = 0.370$) (Tables 1, 2). However, in the endangered taxa this ratio was significantly skewed; the majority of these species (64%) for which ploidy levels are known are diploid, whereas consistent polyploidy was observed in only 36% of these endangered species (Table 1). Interestingly, a substantial proportion of the endangered polyploid taxa (44%) belong to a single family, Orchidaceae. A summary of the test results (Table 2) shows: (1) that diploids and polyploids are equally represented in non-endangered/non-invasive species ($Z = 0.896$; $P = 0.370$); (2) diploids are significantly over-represented in the set of endangered species relative to non-endangered/non-invasive species ($Z = 2.269$; $P = 0.023$); and (3) polyploids are significantly over-represented in invasive species compared with non-invasive/non-endangered species ($Z = 3.131$; $P = 0.001$). Based on these results, the null hypothesis was rejected indicating that diploids were prone to rarity.

The analysis showed that phylogeny has a significant effect on species endangerment. Some of the plant families contained a disproportionate number of endangered species. For example, 31%, 13%, and 32% respectively of the species of Aceraceae, Asclepiadaceae, and Orchidaceae are endangered (Fig. 1A). Including these families in the logistic regression

Table 1. Number of diploid and polyploid species in different conservation status categories of higher plants in the Indian subcontinent

Species status	Diploid (%)	Polyploid (%)
Endangered/rare (*n* = 75)	48 (64)	27 (36)
Invasive (*n* = 43)	12 (27.9)	31 (72.1)
Non-endangered/non-invasive (*n* = 1065)	538 (50.5)	509 (47.8)

Note: Significant departures from the expected ploidy levels recorded in this study as well as suggested in the literature are indicated in Table 2.

Table 2. Summary of results of the test statistics carried out in this study

Type of test	*Z*	*P*-value
Representation of diploids and polyploids in non-endangered species	0.896	0.370
Representation of diploids and polyploids in endangered versus non-endangered/non-invasive species	2.269	0.023*
Representation of diploids and polyploids in invasive versus non-endangered/non-invasive species	3.131	0.001**

* $P < 0.05$; ** $P < 0.01$.

revealed significant terms for specific families, with chromosome number included in the model; these families, therefore, have a high probability of being endangered regardless of their chromosome number (Table 3A). Even with these family differences accounted for, chromosome number is negatively and significantly correlated to the probability of a species being endangered (Fig. 2A). In contrast, phylogeny has no significant effect on invasiveness in this data set and is therefore not included in the regression model for species invasiveness (Fig. 1B). However, chromosome number is positively and significantly related to the probability that a species is invasive (Table 3B). It is evident from Fig. 2B that the species with more chromosomes have a higher probability of being invasive.

DISCUSSION

Many studies on polyploidy and evolution in plants have been published (e.g. Soltis and Soltis, 2000), whereas diploidy has received comparatively little attention from evolutionary biologists. In general, there is a paucity of data on chromosome numbers and not many studies have been carried out recently, as cytology is out of favour. In the Indian subcontinent, chromosome numbers have been reported for 6000 angiosperm species, which is less than 50% of the 17,500 known species (Kumar and Subramaniam, 1985). In the case of the 560 listed endangered species, chromosome counts are known for 75 only, which represents only about 13% of them, or 0.41% of the Indian higher plant flora. This lack of cytological information about endangered species calls for more research efforts, as many species from the subcontinent may go extinct (if they have not done so already) even before their chromosome numbers are known. As chromosome numbers are taxa specific, they could be used as markers or dependable variables to study patterns of rarity and commonness among

Table 3. Logistic regression models of the probability of plant species endangerment (A) and invasiveness (B) on the Indian subcontinent [$n = 1183$ for (A) and (B); model concordance = 87.9% for (A) and 83.9% for (B); log-likelihood value = −274.595 for (A) and −276.986 for (B)]

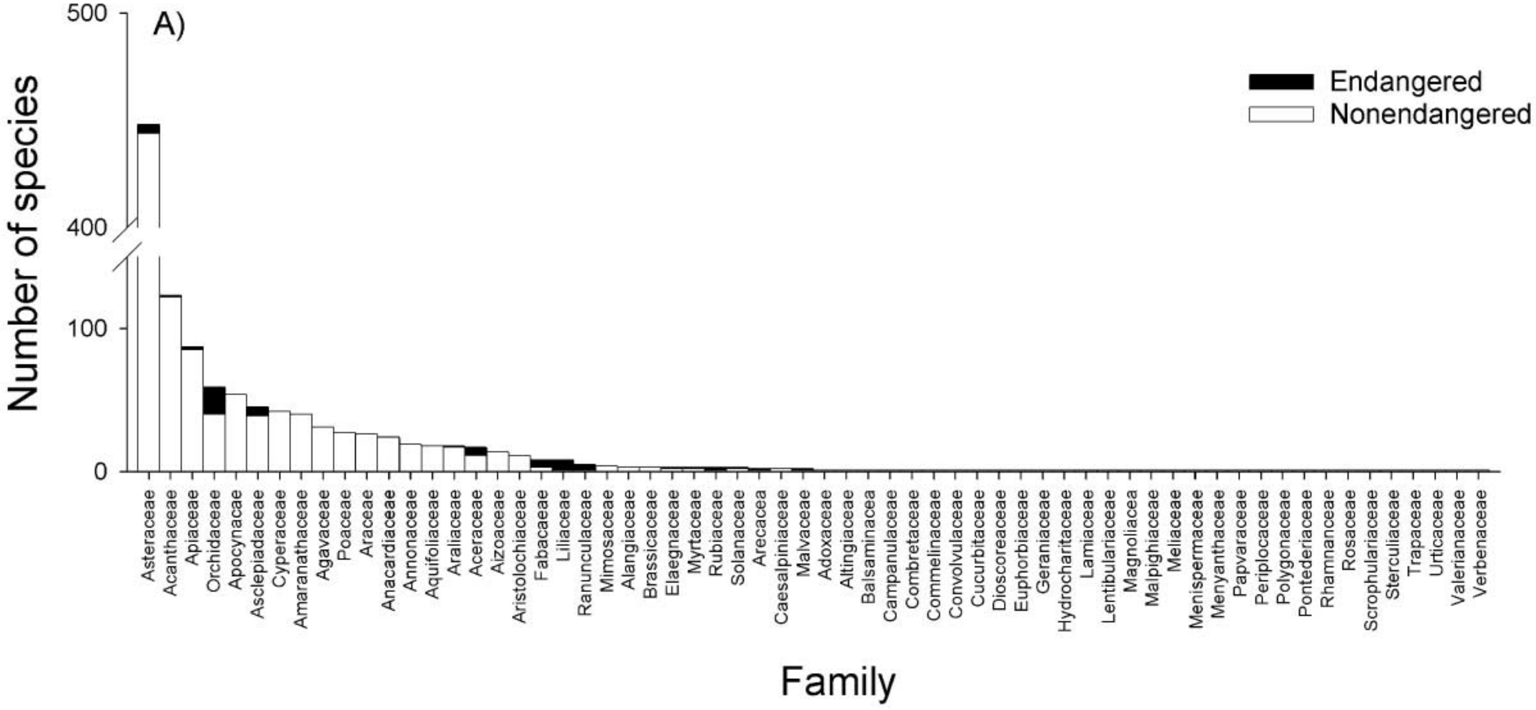
Parameter[#]	Coefficient	P	Odds ratio
(A) Probability of endangerment			
Constant	0.23	0.879	—
Family*			
Aceraceae	3.92	0.001	50.2
Elaegnaceae	4.19	0.009	66.32
Myrtaceae	4.53	0.012	92.66
Orchidaceae	5.76	<0.001	317.18
Chromosome number	−0.18	<0.001	0.83
(B) Probability of invasiveness			
Constant	−12.43	0.278	—
Chromosome number	0.04	0.001	1.05

* Only plant families with significant regression coefficients ($P < 0.05$) are reported.
[#] Family was not included in model (B) because it was not a significant predictor of species invasiveness ($P > 0.05$).

species. My analysis of ploidy levels among plants of the Indian subcontinent indicates that the diploid–polyploid ratio for non-endangered plants follow known trends (Stebbins, 1950; Grant, 1981). However, the chromosome numbers of the endangered taxa show that diploids or species with lower chromosome counts are significantly more likely to be rare than polyploids or species with higher chromosome numbers. This is the first study to report such patterns, and as such it is difficult to predict at this time the reasons behind them. It seems as if diploidy or a low chromosome number has a restrictive control on the evolutionary growth of the species. In contrast, a significant number of the invasive species studied here were found to be polyploids (Table 1). The high levels of polyploidy in invasive species is a relatively well-known phenomenon (Soltis and Soltis, 2000), but the fact that diploidy could have a strong correlation with rarity has to date not been reported.

There is evidence to show that the frequencies of diploidy and polyploidy vary among different plant groups. For instance, about 95% of pteridophytes (ferns and fern allies), 5% of gymnosperms, and 47% of angiosperms are polyploids (Grant, 1981). A closer look at the ploidy levels and conservation status of these plant groups indicates an interesting pattern. For example, in pteridophytes the high frequency of polyploidy could help explain their persistence through geological time. In contrast, more than 95% of gymnosperms are diploid and they are represented by fewer taxa with a higher degree of species rarity (59.23%) than ferns (7.42%) and angiosperms (13.93%) (www.iucn.org/themes/ssc).

It is well known that polyploidy has played an important role in the evolutionary divergence of plant taxa (Stebbins, 1950, 1966), but does it also mean that the taxa left behind in the march of polyploidization face an evolutionary disadvantage? The present findings seem to suggest so, but the exact mechanism of possible negative consequences of diploidy on the persistence of plant species is unclear. Several works have demonstrated the advantages of polyploidy in evolution and persistence of taxa in time and space. These


A)
Endangered
Nonendangered
Number of species
500
400
100
0
Family
Asteraceae
Acanthaceae
Apiaceae
Orchidaceae
Apocynacae
Asclepiadaceae
Cyperaceae
Amaranathaceae
Agavaceae
Poaceae
Araceae
Anacardiaceae
Annonaceae
Aquifoliaceae
Araliaceae
Aceraceae
Aizoaceae
Aristolochiaceae
Fabacaeae
Liliaceae
Ranunculaceae
Mimosaceae
Alangiaceae
Brassicaceae
Elaegnaceae
Myrtaceae
Rubiaceae
Solanaceae
Arecacea
Caesalpiniaceae
Malvaceae
Adoxaceae
Altingiaceae
Balsaminacea
Campanulaceae
Combretaceae
Commelinaceae
Convolvulaceae
Cucurbitaceae
Dioscoreaceae
Euphorbiaceae
Geraniaceae
Hydrocharitaceae
Lamiaceae
Lentibulariaceae
Magnoliacea
Malpighiaceae
Meliaceae
Menispermaceae
Menyanthaceae
Papvaraceae
Periplocaceae
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Rosaceae
Scrophulariaceae
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Trapaceae
Urticaceae
Valerianaceae
Verbenaceae

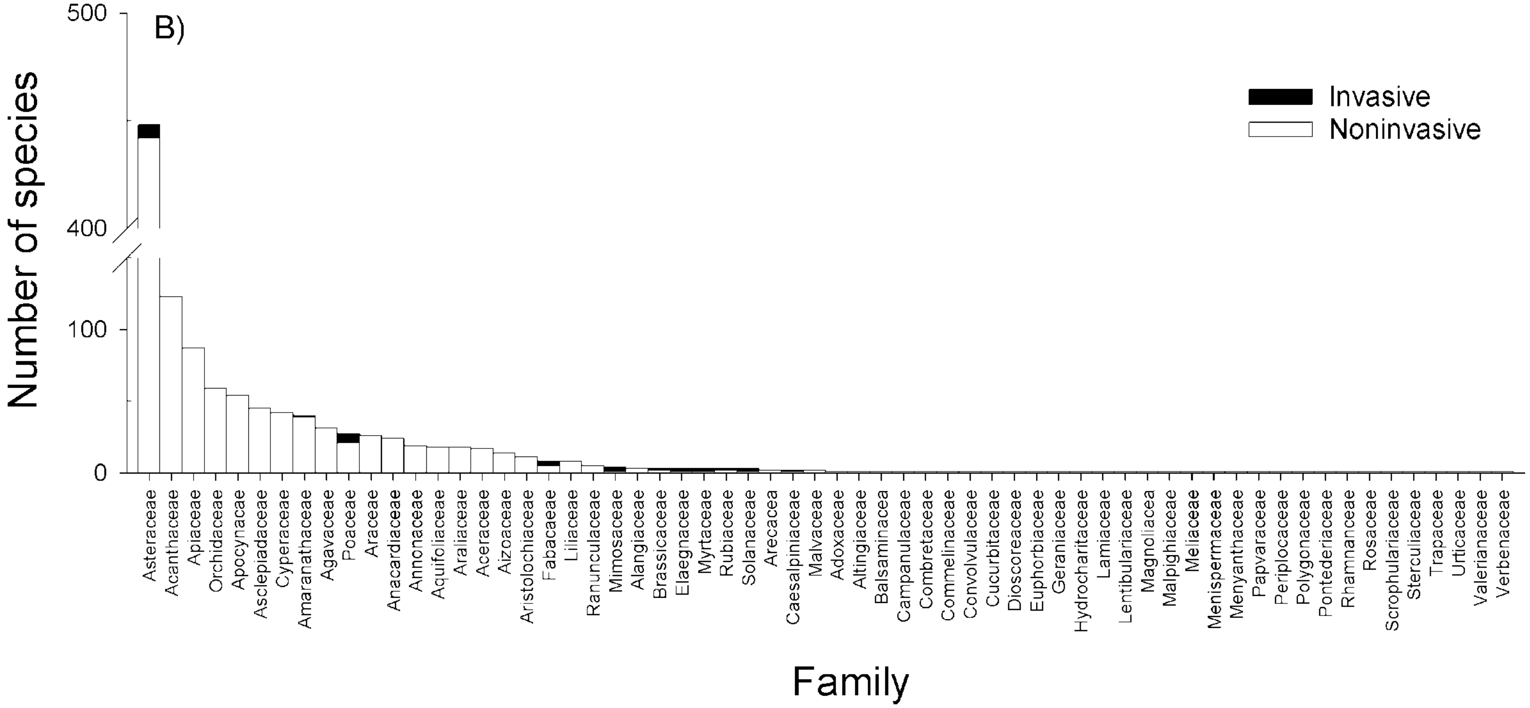

Fig. 1. The proportions of (A) endangered and non-endangered species (y-axis) and (B) invasive and non-invasive species (y-axis) for each family (x-axis).

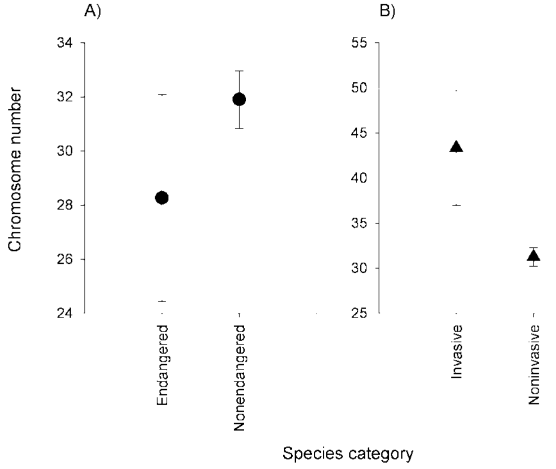

Fig. 2. Mean chromosome number with error (95% confidence interval) bars (y-axis) for (A) endangered and non-endangered species (x-axis) and (B) invasive and non-invasive species.

include higher genetic variability and an ability to adapt to changing environments (Grant, 1981), restoration of fertility in sterile hybrids (Rieseberg, 1995), *in situ* speciation not requiring geographical barriers (Niklas, 1997; Brown and Lomolino, 1998), and the masking of harmful recessive alleles and expression of resistance (Price, 1996). It has been suggested (Glendinning, 1989; Bever and Felber, 1992) that polyploids are less prone to erosion of genetic variation, although research to date on a limited number of species calls this into question (Buza, *et al.*, 2000). Additionally, a serious limitation of the proposed hypothesis may arise from the fact that polyploidy is uncommon in animals, though it has been reported in insects, fishes, and other higher groups (Lewis, 1979). One could argue that in animals both the mechanism of sexual reproduction and species delimitation is well defined, thereby leaving little scope for chromosomal rearrangements and changes. Several studies help to explain the dominance of diploidy in animals favoured by selection (Mable and Otto, 1998; Welch and Meselson, 2000; Weeks, *et al.*, 2001). Polyploidy may not be as prevalent in animals as in plants, but there are references to high chromosome numbers in higher animals as an indicator of evolutionary progress (Grant, 1977). This is one reason to believe that there is a premium on polyploidy or higher chromosome number in the process of evolution and persistence. This study lends support to these observations.

Despite the strong differences in ploidy levels noted here between endangered and non-endangered plants, there was nonetheless a fraction (36%) of endangered species found to be polyploid. These taxa are worth considering, as exceptions to the rule can often be informative. Of the 27 endangered polyploid species, 12 (44%) belong to one family, Orchidaceae. Orchids are commonly known to be extreme habitat specialists (Ozanne, *et al.*, 2003), indicating that the endangered status of these polyploids may be more a result of habitat loss rather than their ploidy levels. If we were to remove these orchid species from the analysis, the significance of the present hypothesis is greatly enhanced, raising the diploid proportion of endangered species from the present 64% to 76%. In addition to the orchids, a number of the remaining endangered polyploids (35%) are narrow endemics, and are taxonomically isolated species, a factor associated with rarity in some analyses (e.g. Hodgson, 1987). Additionally, several external pressures on the habitats of these polyploids are responsible for their endangered status. For instance, *Phoenix rupicola*, an endangered polyploid endemic in the northeast Himalayas and adjoining hills, is a culinary specialty and is heavily exploited. *Clematis theobroma*, *C. bourdillonii* and *Psychotria globocephala*, though polyploids, are narrow endemics faced with serious habitat destruction (Nayar and Sastry, 1987–1990), which may explain their endangered status.

The results presented here provide strong evidence of a relationship between (1) diploidy/low chromosome number and species endangerment and (2) polyploidy/high chromosome number and invasiveness in plant species, at least within the Indian subcontinent. If similar patterns are found elsewhere, they could help guide global conservation efforts. If ploidy levels prove to be reliable indicators of endangerment, plant taxa that are diploid or have low chromosome counts could be targeted as being of potential conservation concern even where full distributional or population data are unavailable. The suggestion by Kunin and Gaston (1993) – if rare species have different properties from common ones, then documenting such patterns will enhance our ability to make informed decisions – seems quite apt and this study attempts to point to one such difference.

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REFERENCES

Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veget. Sci.*, **3**: 187–200.

Bever, J.L. and Felber, F. 1992. The theoretical population genetics of autopolyploidy. *Oxford Surv. Evol. Biol.*, **8**: 185–217.

Brown, J.H. and Lomolino, M.V. 1998. *Biogeography*. Sunderland, MA: Sinauer Associates.

Buza, L., Young, A. and Thrall, P. 2000. Genetic erosion, inbreeding and reduced fitness in fragmented populations of the tetraploid pea *Swainsona recta. Biol. Conserv.*, **93**: 177–186.

Cadotte, M.W. and Lovett-Doust, J. 2002. Ecological and taxonomic differences between rare and common plants of southwestern Ontario. *Ecoscience*, **9**: 397–406.

Fiedler, P.L. 1986. Concepts of rarity in vascular plant species, with special reference to the genus *Calorchotus* Pursh (Liliaceae). *Taxon*, **35**: 502–518.

Gaston, K.J. 1994. *Rarity* London: Chapman & Hall.

Glendinning, D. 1989. Some aspects of autotetraploid population dynamics. *Theor. Appl. Genet.*, **78**: 233–242.

Grace, J.B. and Tilman, D. 1990. *Perspectives on Plant Competition*. San Diego, CA: Academic Press.

Grant, V. 1977. *Organismic Evolution*. San Francisco, CA: W.H. Freeman.

Grant, V. 1981. *Plant Speciation*. New York: Columbia University Press.

Hodgson, J.G. 1986. Commonness and rarity in plants with special reference to the Sheffield flora, Part III. Taxonomic and evolutionary aspects. *Biol. Conserv.*, **36**: 275–297.

Hodgson, J.G. 1987. Why do so few plants species exploit productive habitats? An investigation into cytology, plant strategies and abundance within a local flora. *Funct. Ecol.*, **1**: 243–250.

Klekowski, E.J. and Baker, H.G. 1966. Evolutionary significance of polyploidy in the Pteridophyta. *Science*, **153**: 305–307.

Kubitzki, K. 1975. Relationship between distribution and evolution in some heterobathmic tropical groups. *Bot. Jahrb.*, **91**: 212–230.

Kubitzki, K. 1977. The problem of rare and frequent species: the monographer's view. In *Extinction is Forever* (G.T. Prance and T.S. Elias, eds.), pp. 331–336. New York: New York Botanical Garden.

Kumar, V. and Subramaniam, B. 1985. *Chromosome Numbers of Flowering Plants of the Indian Subcontinent*. Kolkatta: Botanical Survey of India.

Kunin, W.E. and Gaston, K.J. 1993. The biology of rarity: patterns, causes and consequences. *Trends Ecol. Evol.*, **8**: 298–301.

Lewis, W.H. 1979. *Polyploidy: Biological Relevance*. New York: Plenum Press.

Mable, B.K. and Otto, S.P. 1998. The evolution of life cycles with haploid and diploid phases. *BioEssays*, **20**: 453–462.

Nayar, M.P. and Sastry, A.R.K. 1987–1990. *Red Data Book of Indian Plants*, Vols. I–III. Kolkatta: Botanical Survey of India.

Niklas, K.J. 1997. *The Evolutionary Biology of Plants*. Chicago, IL: University of Chicago Press.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L, Körner, C. *et al.* 2003. Biodiversity meets the atmosphere: a global view of forest canopies. *Science*, **301**: 183–186.

Price, P.W. 1996. *Biological Evolution*. Fort Worth, TX: Saunders College Publishing/Harcourt Brace College Publishers.

Purvis, A. and Gittleman, J.L. 2000. Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B*, **267**: 1947–1952.

Purvis, A., Gittleman, J.L., Cowlishaw, G. and Mace, G.M. 2000. Nonrandom extinction and the loss of evolutionary history. *Science*, **288**: 328–330.

Rabinowitz, D., Rapp, J.K., Cairns, S. and Mayer, M. 1989. The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. *Am. Nat.*, **134**: 525–544.

Reader, R.J. 1998. Relationship between species relative abundance and plant traits for an infertile habitat. *Plant Ecol.*, **134**: 43–51.

Rieseberg, L.H. 1995. The role of hybridization in evolution: old wine in new skins. *Am. J. Bot.*, **82**: 944–953.

Schwartz, M.W. 1993. The search for pattern among rare plants: are primitive species more likely to be rare? *Biol. Conserv.*, **64**: 121–127.

Schwartz, M.W. and Simberloff, D. 2001. Taxon size predicts rates of rarity in plants. *Ecol. Lett.*, **4**: 464–469.

Soltis, P. and Soltis, D.E. 2000. The role of genetic and genomic attributes in the success of polyploids. *Proc. Natl. Acad. Sci. USA* **97**: 7051–7057.

Stebbins, G.L. 1950. *Variation and Evolution in Plants*. New York: Columbia University Press.

Stebbins, G.L. 1966. Chromosomal variation and evolution. *Science*, **152**: 1463–1469.

Weeks, A.R., Marec, F. and Breeuwer, J.A.J. 2001. A mite species that consists entirely of haploid females. *Science*, **292**: 2479–2482.

Welch, D.M. and Meselson, M. 2000. Evidence for the evolution of bdelloid rotifers without sexual reproduction or genetic exchange. *Science*, **288**: 1211.