Botanica Orientalis – Journal of Plant Science (2011) 8: 57–69 doi: http://dx.doi.org/10.3126/botor.v8i0.5959 © 2011 Central Department of Botany, Tribhuvan University http://www.nepjol.info/index.php/BOTOR

Research

Habitat differentiation and population traits variation between the rare *Meconopsis napaulensis* and the common congener *M. paniculata*: implications for rare plant management

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Abstract

Understanding the causes of rarity has become increasingly important for the conservation and management of plant species. In this study, we compared spatial distribution, habitat characteristics, and population size and structure of two closely related species of poppy occurring in the Himalaya, the rare and endemic Meconopsis napaulensis and the widespread common congener M. paniculata in order to explain the causes of rarity of the former species. This study was carried out in Langtang National Park, north-central Nepal covering six populations of M. napaulensis and four populations of M. paniculata. Analysis of the habitat features revealed greater tendency of M. napaulensis to exhibit high habitat specificity. It was restricted to nutrient-poor, open and rocky habitats at >3700 m asl. Sites where M. paniculata were sampled showed high variability in terms of edaphic and topographic features. Mean 'area of occupancy' tended to be high for M. paniculata compared to M. napaulensis. M. paniculata showed larger population size and greater abundance as compared to M. napaulensis. The poor representation of younger life stages in M. napaulensis despite high proportion of reproductive adults indicated lower recruitment potential. The present study has illustrated that the rarity of *M. napaulensis* is strongly related to a combination of ecological and geographical constraints, which prevent reproduction, dispersal and colonization. It further demonstrates that the maintenance of population size of rare species largely depends on the survival and abundance of plants of younger stages. Thus, management directed towards reducing the impact on plants of young stages and protecting reproductive individuals from flower and fruit harvesting would help to maintain population size. Finally, development of action plans and guidelines incorporating scientific findings and accommodating local peoples' socio-economic and cultural factors associated with the extinction risks is imperative for the conservation of rare and endemic species.

Key-words: Himalaya, commonness, endemism, extinction risks, habitat amplitude, habitat specificity, rarity.

Introduction

Rarity is a concept that has been explained in terms of abundance, evolutionary history, spatial distribution, and genetic structure of a taxon (for review see Fiedler and Ahouse 1992). Moreover, anthropogenic impacts, such as habitat alteration and over exploitation can lead to or enhance rarity.

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Several criteria have been used to describe patterns of rarity in plant or animal species (Rabinowitz 1981; Rabinowitz *et al.* 1986; Yu and Dobson 2000; Manne and Pimm 2001). Rabinowitz *et al.* (1986), for example, identified seven forms of rarity in the flora of British Isles, based on the dichotomous differences in geographic range (narrow-wide), habitat specificity (wide-narrow) and population size (large-small). More recent works also proposed degree of disjunction, and taxon persistence (short-long) as other criteria for the classi-

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fication of rarity and commonness (Fiedler and Ahouse 1992; Kean and Barlow 2004).

It is predicted that rare species are poor competitors and are generally less abundant, have high habitat specificity and contain small incompatible populations (Cowling 2001). Rare species with their small populations often face greater risks of extinction caused by demographic, genetic and environmental stochastic forces (Shaffer 1981; Gilpin and Soulé 1986). Rarity is thus prescribed as a predictor of vulnerability and a precursor to extinction (Fiedler 1986). Understanding the underlying causes of rarity has become increasingly important for the conservation and management of rare and endemic species. Despite the recognized importance of understanding rarity, the important ecological traits responsible for species rarity are poorly understood for Himalayan plants.

The Himalayan region is known as a hotspot for plant diversity and endemism (Behera *et al.* 2002). Sporadic researches carried out from the Himalaya revealed that the percentage of endemic species range 16-46% in most of the plant groups studied (Dhar 2002; Yoshida 2006). Majority of the endemic species have narrow range of distribution and are considered as rare (Shrestha and Joshi 1996; Dhar 2002; Ghimire 2005; Yosida 2006). The harsh habitat conditions and increased isolation reinforce the rare and endemic species in high altitude habitats of the Himalaya to become highly restricted in distribution.

In this study, we compared spatial distribution, habitat requirements and amplitude, and population size and structure of two closely related species of Himalayan poppy, a rare and endemic Meconopsis napaulensis DC., and a widespread congener M. paniculata (D. Don) Prain (Family: Papaveraceae), in order to explain the causes of rarity of the former species. M. napaulensis is a narrow endemic species restricted to Gosainkunda and Ganesh Himal areas in Rasuwa district, north-central Nepal (Grey-Wilson 2006). M. paniculata, on the other hand, is distributed throughout the Himalaya (Press et al. 2000; Grey-Wilson 2006). The main questions addressed in this study are: (i) do the rare (M. napaulensis) and common (M. paniculata) species differ in terms of spatial distribution, habitat quality, and population size and structure?; (ii) how do the rare and common species differ in their response to variation in habitat conditions?; and (iii) do the constrains to the habitat amplitude and population size explain the rarity of *M. napaulensis*?

Materials and Methods

STUDY SPECIES

Meconopsis napaulensis [recently reinstated by Grey-Wilson (2006)] and M. paniculata are erect monocarpic herbs. M. napaulensis is 0.5 to 1.2 m tall with a slender dauciform taproot, and the whole plant is covered with long barbellete bristles. M. paniculata, on the other hand, is 1 to 4.5 m tall with a thick dauciform taproot to 20-25 mm diameter; the whole plant is covered with stiff barbellete hairs. Aspects of ecology of both the species are poorly known. M. paniculata is one of the common species in the genus, and is widely distributed throughout the Himalaya from NW India to Nepal, Sikkim, Bhutan, NE India and to southern Tibet (Xixang, China) between altitudes of 3000-4400 m asl (Grey-Wilson 2006). It is found growing on various habitats, including closed forests, open woodlands and woodland margins, shrubberies, meadows, rocky alpine slopes, valley slopes and ravines (Sulaiman and Babu 1996; Grey-Wilson 2006). Distribution of M. napaulensis is highly restricted. It is known only from Gosainkunda and Ganesh Himal area and adjoining region in Rasuwa district, north-central Nepal (Grey-Wilson 2006). It is found on rocky and grassy slopes, open shrubberies and stream margins at 3350-4600 (-4880) m asl (Grey-Wilson 2006).

Excavation of some reproductive individuals of both species showed no indication of the presence of distinct underground stem and clonality. Both species depend on sexual means of reproduction. After seed germination, seedlings grow slowly, and for at least four years (personal observation and interview with local herders) plants remain vegetative (rosette stage). After the completion of vegetative rosette stage, plants produce a single stem and branches in April-May. Both species began flowering in June, but the altitude influences the flowering phenology. In M. napaulensis, flowering starts from late June and continues until early August. In M. paniculata, flowering starts slightly earlier, beginning in early June and culminating in late July. In both species, fruiting starts concurrently with flowering and culminates in September. Seeds apparently do not have any specific adaptation for dispersal and stay in the fruit until fruit cover is ruptured or decayed. Plants die at the end of growing season, after completion of reproductive stage.

Members of the genus *Meconopsis* are popular in terms of their ornamental values (Grey-Wilson 2006). In addition, the genus includes some ethnobotanically important plant species, which have been utilized in traditional medicine throughout the Himalaya (Xie *et al.* 2005). The flower, leaf and root of *M. paniculata* are used for the treatment of swelling, diarrhea, fever and cough (Ghimire *et al.* 2008a). The root and leaf of *M. napaulensis* are used to treat digestive system disorders, chest pain, sore throat and headache (personal communication with local people in Lauribina, Langtang National Park, Nepal, 2007 and 2008). The flowers of *M. napaulensis* are used for religious purposes and the seeds of both species are eaten raw by shepherds (Ghimire *et al.* 2008a; personal communication with local people in Lauribina, Langtang National Park, Nepal).

STUDY SITES

The present study was conducted covering different sites (Singompa, Cholangparti, Lauribina and Gosainkund; located between 28°04.290' to 28°06.896' N and 85°20.450' to 85°25.041'E) in Gosaikunda sector within Langtang National Park (LNP) in Rasuwa district, north-central Nepal. The study area covers subalpine to alpine landscapes between 3000-4800 m asl. The landscape is extremely dissected with steep side slopes and comprises glaciofluvial, colluvial and morainal deposits (TRPAP 2005). The seasonal climate is influenced by southern monsoon, which occurs between June to September. Somewhat arctic climate prevails above 4500 m with snowline at 4700 m. Meteorological data of Department of Hydrology and Meteorology, Government of Nepal for the last 7 years (2001-2007) of nearest meteorological station (Dhunche, Rasuwa district; 1950 m asl), showed an average maximum tem-perature of 23.02°C in June and average minimum temperature of 2.22°C in January. Similarly, the average annual precipitation was 1798.64 mm (Department of Hydrology and Meteo-rology, Government of Nepal).

LNP is considered as one of the biodiversity hotspot areas in Nepal. Vegetation within LNP ranges from subtropical and temperate broadleaved and coniferous forests, alpine meadows and scrubs to the nivale zone of dry, scree vegetation. LNP is particularly known to harbor high diversity of rare and endemic taxa of flowering plants. A total of 47 species of national endemic taxa of flowering plants have been recorded within LNP and adjoining areas, out of which 38.3% (18 species) are endemic to this region (Ghimire *et al.* 2008b). Despite the presence of unique flora and vegetation, LNP is experiencing habitat degradation due to high level of anthropogenic impact. The alpine pastures are used for rotational grazing of livestock and harvesting of different resources (Malla *et al.* 1976; Myint *et al.* 2000). Herders migrate with their livestock to alpine pasture in spring and stay in shelters (*goth*), built near pastures mostly located along the trail, and return to their respective village in autumn. The preferred livestock are sheep, horse, yak and *chauri* (crossbreed between yak and hill cow). The main livestock products are meat, wool, milk and *churpi* (dried cheese).

LNP and its bufferzone, inhabited by diverse ethnic groups, are also rich culturally. Many sacred lakes (including the largest one, known as 'Gosainkunda') are found in Gosaikunda sector of LNP, which are religiously significant for both Hindus and Buddhists. Every year, about 25-30 thousand pilgrims, both from Nepal and India, visit Gosaikunda area to worship lord Shiva (LNP/BZMC 2007).

SELECTION OF STUDY POPULATIONS

The whole of the study area with the distribution of populations of selected species was mapped by taking information from the local people and direct field observation. Local people (n = 15) were interviewed by using semistructured questionnaires. Similarly, secondary data was obtained from published flora (Malla et al. 1976) and herbarium specimens housed at TUCH and KATH. Based on the information obtained from field survey, literatures and study of herbarium specimens, a total 13 sites (6 for M. napaulensis and 7 for M. paniculata) each representing distinct population were identified in LNP (Table 1). Out of which, 10 populations, including all 6 populations of M. napaulensis and 4 populations of *M. paniculata* were sampled (Table 1). In each population, individuals of both species occurred in distinct patches, and each such patch was assigned as subpopulation. In total, 26 subpopulations (15 for M. napaulensis and 11 for M. paniculata) were sampled (Table 1). Populations of either of the species were separated from each other due to geographical barrier (such as rocky hill, river), human settlement or they were far apart (mean distance = 1.8 km and 0.9 km, respectively for *M. napaulensis* and *M.* paniculata). In Kyashir Kharka and Brana-Chopche sites (Table 1), the two species were close to each other, but they did not share the same locality as their populations were separated by river.

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| Population/sites No of patch (sub- | | Altitude (m asl) based on | | Latitude | Longitude | Aspect | Habitat type | |
|---------------------------------------|-------------|---------------------------------|------------------|---------------------------|---------------------------|--------|---|--|
| | population) | Previous record [†] | Present study | - | | | | |
| M. napaulensis | | | | | | | | |
| Kyasir Kharka | 2 | - | 3736-3740 | 28°04.290'- 28°04.375' | 85°22.992'- 85°22.892' | S-SW | Riverside habitat with boulder; rocky slope | |
| Brana-Chopche | 2 | - | 3812-3880 | 28°06.892'– 28°06.896' | 85°23.369'– 85°23.600' | NW-SW | Riverside habitat with boulder/gravel; rocky slope | |
| Gosainkunda | 2 | - | 4323-4527 | 28°05.016'- 28°05.107' | 85°25.041'- 85°24.962' | S-SW | Rocky slope | |
| Sarswatikunda | 2 | - | 4110-4260 | 28°04.869'- 28°04.932' | 85°24.015'- 85°23.989' | NE-SW | Rocky meadows | |
| Deurali | 4 | - | 4465-4427 | 28°05.026'- 28°05.056' | 85°24.143'- 85°24.190' | S-SW | Rocky slope | |
| Lauribina-pass | 3 | - | 4418-4484 | 28°05.085'- 28°05.171' | 85°24.015'- 85°23.889' | S-SW | Rocky slope; rocky meadows | |
| M. paniculata | | | | | | | | |
| Singompa [‡] | na | - | 3200-3400 | 28°06.10'- 28°06.634' | 85°20.450'- 85°20.460' | SW | Forest, forest gaps | |
| Kyasir Kharka | 2 | - | 3734-3795 | 28°04.902'- 28°04.940' | 85°23.516'- 85°23.517' | S-SW | Meadows | |
| Cholangpati | 2 | - | 3880-3840 | 28°05.060'- 28°05.067' | 85°23.261'- 85°23.296' | NW-SW | Shrubland; meadows | |
| Lauribina | 3 | - | 3903-3923 | 28°05.120'- 28°05.123' | 85°23.169'- 85°23.166' | NW-SW | Rocky meadows in steep slope | |
| Ghopte [‡] | na | 3960 | - | - | - | - | - | |
| Brana-Chopche | 4 | - | 4055-4078 | 28°05.855'- 28°05.901' | 85°23.530'- 85°23.450' | S-SW | Rocky meadows | |
| Gosainkunda‡ | na | 4260 | - | - | - | - | - | |

| Table 1 | . Populations of | f M. napau | <i>lensis</i> and M | paniculat | a: altitudinal | range, | geographical | position, as | pect and h | abitat tyr |)e(s). |
|---------|------------------|------------|---------------------|-----------|----------------|------------|--------------|--------------|------------|------------|--------|
| | | | | | | <i>U</i> / | | | | ~ ~ ~ | ~ ~ ~ |

[†]Previous record based on Malla *et al.* (1976).

*These populations were not sampled due to either inaccessibility or due to difficulty in locating previously cited populations.

SAMPLING

Each population was visited during the peak growing period in July/August (during monsoon) in 2007 and 2008. In both years, entire area of each subpopulation was extensively surveyed to record all the individual plants, including plants at flowering or fruiting. Based on this information, yearly population size of both species for each population was determined as total number of individuals by combining the value from all respective subpopulations. The 'area of occupancy' of respective species was measured as the spatial area actually occupied by the species in each patch (subpopulation). Sum of the area of all patches for each population gives the total 'area of occupancy' at population level. Similarly, spatial distance between populations was estimated directly in the field and also confirmed by GIS mapping.

In each subpopulation, sampling plots of 100 m² (10 m \times 10 m size) were subjectively placed in the area where the density of plant was high (Burne et al. 2003). The number of such plots varied from 2-4 per subpopulation, depending upon the size of subpopulation. Such a large plot size was used due to very sparse distribution of individuals and relatively gregarious habit of both species. At least one plot per subpopulation was made permanent by marking all the four corners. In each plot, all the individuals of respective species were counted separately, for four stages/size classes, on the basis of plant state and number of leaves: small rosette (1-5 leaves), juvenile rosette (>5-20), large rosette (>20) and mature reproductive (with flowering/fruiting peduncle). In the permanent plot, all the individuals in different size/stage classes were marked separately with aluminium tags. The permanent plots were revisited in July/August 2008 and

monitored for the change in population size and structure. For *M. napaulensis*, among the 15 permanent plots, 4 plots were found almost completely destroyed by livestock grazing. Therefore, subsequent monitoring of these plots was not done.

HABITAT VARIABLES

The habitat parameters studied in each plot included vegetation composition, and soil and topographical features. To obtain vegetation data, we divided the 100 m² plots in to four subplots (each of 25 m² size) and estimated percentage cover for the following: dicotyledonous herbs (excluding Meconopsis), shrubs, monocots (including grass), non-vascular plants (lichen and moss), rock, and bare ground. The plant species were identified based on standard literature (Malla et al. 1976; Polunin and Stainton 1884; Stainton 1988) and comparing with herbarium specimens housed at TUCH. Aspect and altitude of each plot was recorded with the help of compass and altimeter respectively. Latitude and longitude of each plot were recorded with the help of Global Positioning System devise (GPS 400 XL, Megellan, USA). The value of aspect was used to calculate heat load index (HLI) using the following formula (McCune and Grace 2002): HLI = $1 - \cos(\theta)$ (-45)/2; where θ = aspect in degrees east of true north. This index rescales aspect to a scale of zero to one, with zero being the coolest slope (northeast) and one being the warmest slope (southwest) (McCune and Grace 2002).

In each plot, livestock and human harvesting impacts were recorded as a measure of anthropogenic disturbance. Indicators recorded for measuring livestock impact included level of trampling, dung deposition, and levels of plant uprooting, grazing or browsing. Harvesting impact consisted of two variables: levels of flower and fruit harvesting (scar left after plucking of flowers/fruits were used as indicators of harvesting impact). In addition, natural impact was recorded by observing landslide, fallen rocks and river damage. Each type of disturbance was scored by assigning categorical value as 0 (no disturbance), 1 (low disturbance), 2 (moderate disturbance), 3 (high disturbance), and 4 (very high disturbance).

Soil depth was measured by inserting iron peg in the four corners and one centre point of each plot; and based on these, mean soil depth per plot was calculated. Six soil samples (at least one sample directly below the canopy of respective species), from the rooting depth (5-15 cm), were collected from each subpopulation. The soil samples were

homogenously mixed to obtain a single sample (300 g) per subpopulation. The soil samples were air dried in shade for up to 15 days and stored in airtight zip-lock plastic bags until laboratory analysis. The samples were analyzed for pH, organic matter (OM) and nitrogen (N) in Soil Management Directorate, Department of Agriculture, Government of Nepal, Lalitpur, Nepal. Potentiometric titration method was used to determine pH. OM was determined by Walkley-Black method; soil N, in the form of ammonium, was analyzed by using modified Kjeldahl method (PCARR 1980).

DATA ANALYSIS

Both the parametric and non-parametric statistical tests were performed to analyze the data. Non-parametric tests were performed if the data (even after transformation) did not meet normality and homogeneity of variance. Spatial area occupied by M. napaulensis and M. paniculata and the number of reproductive and total individuals of both species at different scale (plot, subpopulation and population) and time were compared based on independent sample t-test. Kolmogorov-Smirnov Z test was used to analyze differences in population structures between two species. Non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) and associated pair wise comparisons (Mann-Withney U tests) were performed to detect differences in the subset of habitat parameters between species and among their populations. Coefficient of variation (CV) was calculated, as the ratio of the standard deviation to the mean, for all habitat variables to detect the extent of variability within the selected species (Sokal and Rohlf 1995).

All the variables related to human harvesting, livestock and natural disturbances were separately combined by using Principle Component Analysis (PCA) to obtain overall measure of livestock, harvesting and natural impacts respectively. In each of these cases, single principle component was obtained explaining 80.3%, 71.5% and 67.1% variances respectively. In all these combined cases, PCA-factor scores were used as predictor variables in multivariate analyses (see below) which allowed us to control for the effect of multicoliniarity. Linear regression analyses (enter method) were carried out to assess whether the different types of anthropogenic impacts (human harvesting and livestock) were related to altitude and distance from trail and nearest *goth* (livestock assembly point), where human or livestock activities are expected to be high.

| Habitat attributes | | M. napaulensis | | | M. paniculata | | Species |
|--|--------------------------|-----------------------|---|---------------------------|----------------------|--|---|
| | Mean ± SD | CVb | Population difference ^c χ^2 | Mean±SD | CVc | Population difference $^{\mathcal{X}^2}$ | difference^d 'p' based on Mann- Whitney U-test |
| Altitude (masl) ^a | 4260.33 ± 292.17 | 6.86 | 18.69^{**} | 3930.12 ±118.37 | 3.01 | 14.87** | 0.001 |
| Heat load index | 0.94 ± 0.078 | 8.25 | 7.42 | 0.43 ± 0.42 | 97.67 | 10.43^{*} | <0.001 |
| Non vascular cover (%) | 3.85 ± 1.32 | 34.31 | 4.34 | 11.09 ± 4.29 | 38.68 | 8.58* | <0.001 |
| Herb cover (%) | 50.11 ± 4.92 | 9.81 | 2.86 | 70.82 ± 31.99 | 45.17 | 9.46* | 0.001 |
| Monocot cover (%) | 12.63 ± 1.67 | 13.20 | 4.61 | 16.53 ± 5.14 | 31.09 | 9.43* | 0.001 |
| Shrub cover (%) | 12.33 ± 1.73 | 14.04 | 8.51 | 48.94 ± 9.67 | 19.76 | 11.92^{**} | <0.001 |
| Total vegetation cover (%) | 78.93 ± 4.29 | 5.43 | 5.93 | 147.35 ± 43.95 | 29.83 | 13.72^{**} | <0.001 |
| Rock cover (%) | 62.41 ± 2.55 | 4.08 | 8.64 | 14.88 ± 7.17 | 48.19 | 11.38^{*} | <0.001 |
| Bare soil cover (%) | 16.67 ± 3.10 | 18.61 | 12.16^{*} | 9.82 ± 5.17 | 52.65 | 8.24* | <0.001 |
| Species richness (per 0.01 ha plot) | 21.37 ± 2.53 | 11.83 | 6.94 | 22.76 ± 4.4 | 19.33 | 8.91^{*} | su |
| Soil depth (cm) | 7.53 ± 0.18 | 2.44 | 2.60 | 15.11 ± 3.3 | 21.99 | 5.69 | <0.001 |
| Soil pH | 4.85 ± 0.43 | 8.94 | 5.17 | 5.11 ± 0.72 | 14.13 | 7.55 | SU |
| Soil organic matter (%) | 7.31 ± 3.12 | 42.66 | 8.93 | 11.27 ± 5.49 | 48.70 | 6.54 | 0.051 |
| Soil nitrogen (%) | 0.36 ± 0.15 | 40.95 | 7.12 | 0.56 ± 0.28 | 49.02 | 6.54 | 0.037 |
| Livestock impact ^e | 2.73 ± 1.19 | 43.52 | 16.41^{**} | 2.78 ± 0.64 | 23.13 | 12.40^{**} | SU |
| Harvesting impact ^e | 2.35 ± 1.34 | 56.81 | 15.20^{*} | 2.29 ± 0.90 | 39.34 | 3.87 | ns |
| Overall anthropogenic disturbance ^e | 2.60 ± 1.20 | 46.02 | 14.20^{*} | 2.62 ± 0.66 | 25.12 | 8.14* | ns |
| Overall natural impact ^e | 1.43 ± 0.42 | 29.46 | 4.01 | 0.94 ± 0.67 | 71.13 | 15.36^{**} | 0.038 |
| ^a <i>M. paniculata</i> occurred at an elevatior | n range of 3200-4078 m a | ısl., but populations | growing at and below | tree line (3200-3700 m a: | sl) were excluded fo | or detail study. | |

Table 2. Habitat characteristics of *M. napaulensis* and *M. paniculata*.

Significance test to detect differences among populations of a species in the subset of environmental variables based on non-parametric Kruskal-Wallis one-way ANOVA (n = 27 and 17; df = 5 and 3

CV= coefficient of variation within the species among their populations.

for *M. napaulensis* and *M. paniculats*, respectively); chi-square (χ^2) values followed by an asterisk indicate that the medians for a particular environmental variable among populations of a species are

significantly different from one another at *p < 0.05, **p<0.01 or *** p<0.01 kvel, x² values not followed by an asterisk indicate that the medians are statistically insignificant among populations)

Significance test to detect differences between rare and common species of Meconopsis in the subset of environmental variables based on Mann-Whitney U tests; only significant p values are shown (ns

= the difference was not significant at p = 0.05 level).

"Livestock impact represents combination of four variables: kevel of trampling, dung deposition, damage by uprooting and grazing or browsing. Harvesting impact represents combination of two variables: level of flower and fruit harvesting. Overall anthropogenic disturbance represents combination of both livestock and human harvesting impacts. Natural impact represents combination of three variables:

landslide, rock falling and river damage (each type of disturbance was scored by assigning categorical value as 0 = no disturbance to 4 = high disturbance).

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Figure 1. DCA ordination of sample plots from the study sites of two species of *Meconopsis* (length of the gradient = 2.90 and 1.63; and eigenvalue = 0.53 and 0.14 for the first and second axis respectively; the first two DCA axes cumulatively explained 66.8% of variance in species data; cover values of both species were deleted before analysis). Symbols refer to sample plots from sites where *M. napaulensis* and *M. paniculata* occured.

Detrended correspondence analysis (DCA), on its default setting and down weighting rare species, was performed to assess the extent of compositional variations between the sites of two species (McCune and Mefford 1999). Percent cover value of 59 species (excluding *Meconopsis* spp.) from 44 plots (response variables) were used in DCA. The multivariate analysis was performed with PC-ORD Version 4.25 (McCune and Mefford 1999) and the rest of the analyses were performed with SPSS version 11.5 (SPSS Inc., Chicago, USA).

Results

DISTRIBUTION AND HABITAT DIFFERENTIATION

The two species existed in different localities even in the nearest sites. Three populations of *M. paniculata* and two of *M. napaulensis* occupied subalpine–alpine ecotone (3700-3900 m) with similar climatic and physiographical conditions, although the two species did not co-occur at the same locality. The closest populations of the two species from subalpine–alpine ecotone were located almost at a distance of 0.8 km. The rare species (*M. napaulensis*) was mostly confined to fairly high altitude (>4000-4500 m, 4 populations), whereas, only one population of *M. paniculata* was recorded above 4000 m (Table 1). The habitats of the two species differed

significantly for 13 out of 18 variables studied (Table 2). The common species (M. paniculata) occurred mainly in habitats with relatively closed vegetation cover with well-drained nutrient-rich sandy-loam soil (Table 1, 2). It was recorded from upper temperate and subalpine forests, subalpine and alpine meadows, rocky slopes, and shrubland dominated by dwarf Rhododendron spp. and Berberis spp. Most of the study populations of M. napaulensis, on the other hand, were restricted to high altitude steep rocky slopes, riverside rocky habitats or rocky meadows with nutrient-poor substrates. The restricted distribution of *M. napaulensis* in nutrient poor, well exposed (dry), open, rocky habitat is well illustrated by small coefficients of variation (CV) for soil nutrients, heat load index, overall vegetation cover and rock cover, respectively (Table 2). The CVs for most of these variables were more than four fold in M. paniculata growing sites.

Although plant communities in the study sites where M. napaulensis and M. paniculata occurred were dominated by herbaceous species, with almost equal species richness (Mann-Whitney U-test, U = 199.5, p = 0.465), these differed markedly in terms of stand structure and composition (Table 2, Figure 1). The DCA ordination clearly showed the differences in compositional variation between the habitats of two species (Figure 1). The sample plots of M. paniculata and M. napaulensis sites were clearly separated in the first DCA axis. Sample plots with M. paniculata were clustered towards the negative end and those with M. napaulensis were clustered towards the positive end of the first DCA axis. Percentage vegetation cover and cover of rock and bare soil significantly differed between the sites where these two species were studied (Table 2). Cover values of all functional groups (non-vascular, dicotyledonous herbs, monocotyledons herbs and grasses, and shrubs) were significantly higher in M. paniculata growing sites; whereas values of rock and bare ground cover were significantly higher in M. napaulensis growing sites (Table 2). Low vegetation cover in the M. napaulensis growing sites indicates decreased inter-specific competition with surrounding vegetation.

The heat load index was very high for sites where *M. napaulensis* occurred, as this species was highly specific to more inclined landscape with exposed rocky slopes receiving more solar radiation as compared to *M. paniculata*, which occurred in variable habitats (Table 2). Among the edaphic variables, values of soil depth, OM and N were higher in *M. paniculata* than in *M. napaulensis* growing sites.

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Table 3. Relationships between distance from major human or livestock activities (considered as independent variables) and different types of anthropogenic impact in *M. paniculata* (df = 16) and *M. napaulensis* (df = 26) growing sites based on linear regression analysis. Only significant (p<0.05) explanatory variables are given. R² is the adjusted coefficient of determination; beta is the standardized regression coefficient.

| Predictor variables* | Impact types (response variables)‡ | Ad. R ² | Beta | t | Р |
|----------------------------|------------------------------------|--------------------|--------|--------|---------|
| M. napaulensis | | | | | |
| Distance from trail | Livestock impact | 0.844 | -0.922 | -11.89 | < 0.001 |
| | Human harvesting | 0.735 | -0.863 | -8.55 | < 0.001 |
| | Overall anthropogenic impact | 0.863 | -0.932 | -12.83 | < 0.001 |
| Distance from nearest goth | Livestock impact | 0.423 | -0.667 | -4.48 | < 0.001 |
| | Human harvesting | 0.358 | -0.619 | -3.94 | 0.001 |
| | Overall anthropogenic impact | 0.428 | -0.671 | -4.52 | < 0.001 |
| Altitude | Livestock impact | 0.607 | 0.789 | 6.42 | < 0.001 |
| | Human harvesting | 0.495 | 0.717 | 5.15 | < 0.001 |
| | Overall anthropogenic impact | 0.616 | 0.794 | 6.53 | < 0.001 |
| M. paniculata | | | | | |
| Distance from trail | Livestock impact | 0.576 | -0.776 | -4.76 | < 0.001 |
| | Human harvesting | 0.240 | -0.537 | -2.46 | 0.026 |
| | Overall anthropogenic impact | 0.525 | -0.745 | -4.32 | 0.001 |
| Distance from nearest goth | Livestock impact | 0.404 | -0.665 | -3.44 | 0.004 |
| | Human harvesting | 0.320 | -0.602 | -2.92 | 0.011 |
| | Overall anthropogenic impact | 0.480 | -0.716 | -3.97 | 0.001 |

*Variables were log transformed before analysis.

[‡]In each case, PCA factor scores were used which were extracted (in all cases 1 component was extracted) combining all disturbance variables related to respective impact type.

Habitats of both species received almost equal anthropogenic disturbance, but natural impact was significantly high in M. napaulensis than in M. paniculata growing sites (Mann-Whitney U-test, p = 0.038) (Table 2). The main anthropogenic disturbance for both species included livestock grazing, trampling, and collection of flowers and capsules for medicinal and religious purposes. All the studied populations of M. paniculata experienced same level of human harvesting impact $(\chi^2 = 3.87, p > 0.05)$, but the harvesting impact differed significantly among the populations of *M. napaulensis* (χ^2 = 15.20, p < 0.01). The livestock impact differed significantly among the populations of both species ($\chi^2 = 16.41$ and 12.40 for M. napaulensis and M. paniculata respectively, in both cases p < 0.01). In both cases, anthropogenic impact showed significant negative linear relationship with spatial distance from hiking trail and temporal pastoral settlements (goth) (Table 3). In addition, there was significant positive linear relationship between altitude and various types of anthropogenic and natural disturbances in M. napaulensis growing sites (Table 3). In Kysir-kharka and Brana-Chopche sites of low

altitude, *M. napaulensis* experienced low anthropogenic pressure, whereas high altitude sites such as Gosaikunda and Sarswatikunda, received high anthropogenic disturbance.

POPULATION SIZE AND STRUCTURE

Mean 'area of occupancy' at the level of population and subpopulation (patch) tended to be high for *M. paniculata* (population mean area = 4.31 ha; subpopulation mean area = 1.57 ha) compared to *M. napaulensis* (population mean area = 3.18; subpopulation mean area = 1.27), although between species difference in area of occupancy was statistically insignificant (Table 4). Despite this similarity, both species differed markedly in terms of population size and abundance. Both in 2007 and 2008, the number of reproductive and total individuals was higher for common species (*M. paniculata*) than for rare species (*M. napaulensis*) at all the spatial scales (population, patch and plot) (Table 4). Mean population size of *M. paniculata* (considering all stage classes) was 274.75 and 287.75 individuals in 2007 and 2008 respectively; whereas

Table 4. Spatial area occupied by *M. napaulensis* and *M. paniculata* and number of their reproductive and total individuals at the population, patch (subpopulation) and plot levels in 2007 and 2008 [plot-wise number based on data from permanent plots (each of 10 m \times 10 m)].

| Variables | M. napau | lensis | M. panic | Species difference | | |
|---|------------------|------------|------------------|--------------------|--------|---------|
| | Mean ± SE | Range | Mean ± SE | Range | t | Р |
| Mean area occupied by patch/subpopulation (ha)* | 1.27 ± 0.18 | 0.4-3 | 1.57 ± 0.64 | 0.36-7.79 | 0.449 | 0.662 |
| Mean area occupied by population (ha)‡ | 3.18 ± 0.77 | 0.85-5.935 | 4.31 ± 1.83 | 1.32-9.63 | 0.574 | 0.596 |
| Population-wise no. of rep. individuals in 2007‡ | 26.00 ± 5.63 | 11-51 | 41.75 ± 8.07 | 24-63 | 1.826 | 0.107 |
| Population-wise no. of total individuals in 2007 [‡] | 137.17 ± 26.54 | 65-254 | 274.75 ± 47.78 | 169-388 | 2.827 | 0.023 |
| Population-wise no. of rep. individuals in 2008 [‡] | 40.33 ± 9.60 | 16-81 | 55.00 ± 8.75 | 31-68 | 1.345 | 0.216 |
| Population-wise no. of total individuals in 2008 [‡] | 116.67 ± 27.38 | 61-245 | 287.75 ± 44.27 | 184-387 | 3.803 | 0.005 |
| Patch-wise no. of rep. individuals in 2007* | 10.4 ± 1.23 | 5-25 | 15.18 ± 3.57 | 8-50 | 1.670 | 0.112 |
| Patch-wise no of total individuals in 2007* | 54.87 ± 4.12 | 29-96 | 99.91 ± 18.59 | 59-280 | 3.626 | 0.002 |
| Patch-wise no. of rep. individuals in 2008* | 9.33 ± 1.88 | 0-28 | 17.55 ± 3.96 | 8-56 | 2.635 | 0.016 |
| Patch-wise no. of total individuals in 2008* | 46.67 ± 5.78 | 19-112 | 104.64 ± 17.52 | 67-274 | 5.016 | < 0.001 |
| Plot-wise no. of rep. individuals in 2007 [¥] | 3.08 ± 0.26 | 2-5 | 3.00 ± 0.23 | 2-4 | -0.238 | 0.814 |
| Plot-wise no of total individuals in 2007¥ | 10.50 ± 0.70 | 7-16 | 18.36 ± 1.27 | 12-26 | 5.406 | < 0.001 |
| Plot-wise no. of rep. individuals in 2008¥ | 2.83 ± 0.30 | 1-5 | 4.45 ± 0.45 | 3-8 | 2.985 | 0.008 |
| Plot-wise no. of total individuals in 2008¥ | 8.42 ± 0.67 | 6-13 | 19.64 ± 1.02 | 14-27 | 9.199 | < 0.001 |
| | | | | | | |

n = 15 (*M. napaulensis*), n = 11 (*M. paniculata*); n = 6 (*M. napaulensis*), n = 4 (*M. paniculata*); n = 12 (*M. napaulensis*), n = 11 (*M. paniculata*).

the value for *M. napaulensis* was 137.17 and 116.67 respectively (Table 4). Analysis of plot level data revealed significantly higher density of *M. paniculata* (overall mean density 1829.41 and 1963.6 plants ha⁻¹ in 2007 and 2008 respectively) compared to *M. napaulensis* (1077.78 and 841.67 plants ha⁻¹ respectively) in both the years, i.e. 2007 ($t_{42} = 6.732$, p < 0.001) and 2008 ($t_{21} = 5.532$, p < 0.001). Density of both species did not vary much among studied populations (data not shown).

The two species markedly differed in the structure of their populations (Figure 2). While *M. napaulensis* exhibited almost 'J' pattern of population structure with a gradual increase in size class, *M. paniculata* showed high proportions of intermediate life stages exhibiting almost unimodal population structure (Figure 2). These results indicated that younger life stages (small and juvenile rosettes) were poorly represented in *M. napaulensis* populations despite high proportions of reproductive adults. We found significantly lower rejuvenation (expressed as the sum of small rosette and juvenile rosette density divided by the density of the reproductive adults) in *M. napaulensis* (1.33) than in *M. paniculata* (2.41) (Z = 2.632, p < 0.001).

For both species, the proportion of different life stages did not differ significantly among studied populations. In the

case of *M. napaulensis*, temporal variation in population structure was also not found. Population structure of *M. paniculata*, on the other hand, was significantly different between two study years; while proportion of juvenile rosettes was decreased (Z = 2.584, p < 0.001), the proportion of small rosettes increased significantly (Z = 1.423, p = 0.0347), but proportions of other life stages did not change much.

□ Small rosette
Upper Juvenile rosette
Large rosette
Reproductive



Figure 2. Population structure (proportion of individuals in different stage/size classes) of *M. napaulensis* and *M. paniculata* (mean of 2007 and 2008; n = 39 and 28 respectively for *M. napaulensis* and *M. paniculata*). Bars with different letters in each stage/size class between species represent significant difference at p<0.05 level based on Kolmogorov-Smirnov Z test.

Discussion

ECOLOGICAL REQUIREMENTS AND HABITAT AMPLITUDE The two closely related species of Meconopsis considered in the present study vary in their habitat requirements and amplitudes. They did not co-occur in the same locality even some of their nearest populations were present in similar climatic and physiographic conditions of subalpine-alpine ecotonal habitats. This supports the idea that the difference in rare and common species is strongly related to ecological (microhabitat) separation. Microhabitat specialization limits the distribution of rare species (Maliakal-Witt et al. 2005). According to Bazaaz (1991), 'habitat selection for plants results from evolutionary adjustment of species to environmental factors so that the species functions better in some habitats than in others'. However the ability of a species to occupy preferred habitat patch is influenced greatly by their inherent characteristics, such as dispersal and establishment abilities (Hegde and Ellstrand 1999; Burne et al. 2003). Barriers and constraints on dispersal can prevent a species from occupying perfectly suitable habitats (Holt 2003).

Analysis of the habitat features of two species of Meconopsis revealed greater tendency of M. napaulensis to exhibit high habitat specificity. M. napaulensis, like other narrow endemic species (Kruckeberg and Rabinowitz 1985; Debussche and Thompson 2003), was found mainly associated with extreme edaphic conditions (nutrient-poor, dry, open and rocky substrates of high altitudes) where competition from dominant vegetation is reduced. Soil acidity, amount of nitrogen, and organic matter did not vary much among study sites where M. napaulensis occurred. M. paniculata sites, on the other hand, showed high variability in terms of edaphic and topographic features. Higher values of CV for most of the habitat variables in the case of M. paniculata compared to M. napaulensis further indicates high habitat variability among the sites where the former species occurred. M. paniculata, thus, can be considered as habitat generalist. Ecological study of Meconopsis spp. in Sikkim Himalaya by Sulaiman and Babu (1996) also suggested M. paniculata as a habitat generalist species. M. napaulensis, on the other hand, with low CV for most of the habitat variables, exhibited narrower habitat amplitude and therefore can be considered as habitat specialist. Habitat specialization is considered as an important determinant of range limits (MacArthur 1972) and widely cited as a potential cause of species rarity (Kruckeberg and Rabinowitz 1985; Hodgson 1986; Debussche and Thompson 2003).

DISTURBANCE

In the Himalayas, Meconopsis spp. are facing human-induced habitat destruction due to livestock grazing and plant part harvesting. Local people in Gosaikunda area collect different plant parts (roots, leaves, flowers, fruits and seeds) of both species for medicinal, religious and edible purposes. The present study has demonstrated increasing anthropogenic disturbance with increasing altitude, as the extent of pastoral land is high at high altitude with high livestock activity (Fox et al. 1996) during plants' peak growing period. People move their livestock to alpine pastures for grazing in summer season, during which period herders also collect important medicinal plants, including parts of Meconopsis spp. Most of the populations of M. napaulensis are located along the trekking route (from Lauribina to Gosainkunda), thus they received higher level of grazing, trampling and harvesting pressures. Thousands of pilgrims traveling to holy Gosainkunda Lake (located at ca. 4000 m asl), especially during 'Janai purnima' (a festival of Hindus that is celebrated every year in August), also prefer flowers of M. napaulensis for offering to the deities of this lake (personal interview with local people), harvesting more flowers from high altitude sites. Although the rosette plants of M. napaulensis are not much preferred by cattle due to plants' bitter taste, sheep and horse were observed to graze the plants at high altitude. The rosette leaves remain green throughout the year (Grey-Wilson 2006), in dry season when the rest of the dominant grasses and forbs are dry and unpalatable, Meconopsis rosettes remain the preferred food for herbivores. Environmental variables, including human activities, have strong influence on richness and abundance of rare alpine plants (Ghimire et al. 2006). The abundance of plants in alpine habitat may show positive correlation, to a certain extent, with low grazing activities (Ghimire et al. 2006), but combination of grazing and harvesting have strong negative effect on highly rare species, such as *M. napaulensis* (see below).

POPULATION SIZE AND STRUCTURE

Present study showed larger population size and greater abundance of geographically widespread common species (*M. paniculata*) compared to geographically restricted rare species (*M. napaulensis*). Lower abundance and small population size are common features of many rare species (Witkowski *et al.* 1997; Burne *et al.* 2003). Previous studies (e.g., Byers and Meagher 1997; Burne *et al.* 2003; Dickinson *et al.* 2007) have demonstrated the difference in abundance of rare species and their widespread congeners to be related to the difference in the ability of viable seed production, and their dispersal, recruitment and competitive abilities, among others. Although dispersal abilities were not compared in the present study, preliminary observations suggest that both species had equal opportunities for seed dispersal by wind or water, as they produced very light seeds, the size of which did not vary much between the species (Ghimire and Poudeyal in prep.). However, the strong mountain barriers and increased isolation at high altitude restricts dispersal in M. napaulensis compared to *M. paniculata* thus preventing the plant from occupying suitable habitats. In some locations, pikas (Ochotona sp.) were found to feed on capsules of M. napaulensis. The diet of pika is known to vary with the season; at higher elevations, they may feed upon flowers, berries and leaves of alpine plants (Khanal 2007). Some opportunistic seedlings were seen growing in the rock crevices near the burrows of this animal, but due to the lack of suitable microhabitat, the seedlings did not grow well. The lower abundance of M. napaulensis is, therefore, not only related to limited dispersal but can also be attributed to its lower potential for viable seed production (Ghimire and Poudeyal in prep.), low seedling recruitment capacity and their low competitive ability (see below).

The poor representation of younger life stages in M. napaulensis populations despite high proportions of reproductive adults indicate low recruitment potential. Significantly lower rejuvenation (expressed as the sum of small rosette and juvenile rosette density divided by the density of the reproductive adults) found for M. napaulensis clearly illustrates that the recruitment of this species was much more reduced than that of common species (M. paniculata). Dry and rocky habitat, typical of M. napaulensis can be attributed to be unsuitable for successful recruitment and seedling establishment. Availability of seeds on safe sites and suitable environment are critical for seedling recruitment and establishment in harsh habitats, such as in alpine areas (Happer 1977; Baskin and Baskin 1998; Quilichin and Debusshche 2000). Studies have reported physiological dormancy in seeds of Meconopsis spp., and such dormancy is broken down naturally by winter stratification (Sulaiman 1993; Dar et al. 2009). In addition, seeds of Meconopsis spp. are short-lived (about a year, Ghimire and Poudeyal in prep.), thus all buried seeds loose viability within a year when suitable environmental conditions are not met. Thus very low seedling recruitment in the case of *M. napaulensis* may be due to factors limiting viable seed production and safe site availability.

Many studies have demonstrated positive associations between geographic range size and abundance for closely related species across many taxa; widespread species are reported to exhibit high local abundance, but narrowly distributed species are more sparse (Brown 1984; Gaston and Lawton 1990). However, rare species studied by others also showed higher local abundance than their widespread congeners (Simon and Hay 2003; Lesica et al. 2006). Murray and Lepschi (2004) found that most of the locally rare plant species (91% of 57) of open forest occurred in higher abundance at other sites within their geographical range (somewhere-abundant species), while the remaining small percentage of locally rare species were consistently rare (everywheresparse species). Thus, as compared to geographically widespread congener (M. paniculata), the rare M. napaulensis can be classified, based on Rabinowitz (1981) criteria, as having narrow range, and being habitat-specific and locally sparse.

In conclusion, the rarity of *M. napaulensis* is strongly related to a combination of ecological and geographical constraints, which prevent reproduction, dispersal, colonization and establishment. The major ecological constraints are related to narrow habitat amplitude and smaller population size. The harsh habitat conditions, limited safe site availability for seedling establishment and poor competitive ability might have lead *M. napaulensis* to become highly restricted in distribution. The geographical constraints are related to small range size and extreme isolation of its populations. The small range size of rare endemic species could also be linked to their age (Lesica *et al.* 2006; Dickinson *et al.* 2007). It can be expected that such species has not yet been able to spread to their full potential as they have speciated more recently than their widespread congeners.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

The present study provided information on key similarities and differences in habitat conditions between two closely related species of *Meconopsis* that differ in abundance. Although this study could not represent accurately long-term pattern in the recruitment and change in population size but it serves as the first step towards understanding the factors likely limiting the rare species. Basically, the data pertaining to geographical distribution and habitat conditions can be valuable for locating populations of both species and identifying optimal ecological conditions for management. Similarly, population size and structure of both species can be valuable as tool for quick assessment of the viability of plant populations and formulate short-term strategy for management. However, detail demographic study of *M. napaulensis* is needed in the future to predict the long-term viability of its populations.

The ecological and geographical constraints associated with reduced seedling recruitment, establishment and colonization in rare species (M. napaulensis) in turn reduce the viability of populations and make their recovery after any disaster, difficult. This ultimately make them highly vulnerable to local extinction after natural catastrophe or human disturbance. Maintenance of population size of M. napaulensis largely depends on the survival and abundance of plants of young stage. Thus, management directed towards reducing the impact on young stages would enhance the survival of young life stages and this in turn would help to maintain the population size of rare species. In addition, mature plants should also be strictly protected from flower and fruit harvesting to enhance reproductive output. In this regard, development of action plans and guidelines incorporating scientific findings and accommodating local peoples' socioeconomic and cultural factors associated with the extinction risks of plant species is imperative for the conservation and proper management of rare and endemic species.

Acknowledgements

We are thankful to the authorities of Langtang National Park and Department of National Park and Wildlife Conservation of Ministry of Forest and Soil Conservation, Government of Nepal for granting permission to carry out this work within the protected area. We would also like to express our sincere thank to the local people of Gosaikunda area for their support and for sharing their knowledge about the study species. We thank N.P. Pokhrel for his help during the field work.

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