

Demographic variation and population viability in a threatened Himalayan medicinal and aromatic herb *Nardostachys grandiflora*: matrix modelling of harvesting effects in two contrasting habitats

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Summary

1. Despite significant interest in the sustainable use of medicinal plants, the population ecology of many medicinal plant species remains unstudied. Also, few demographic studies have compared effects of harvesting across habitats. We studied the demography of a highly threatened perennial Himalayan medicinal herb, *Nardostachys grandiflora*, in two habitats and examined effects of indigenous harvesting regimes on its population dynamics.

2. In a rocky-outcrop population in 1998, different levels of rhizome harvesting were applied directly by the local users. In meadows, we sampled an unharvested population and another population that was commercially harvested. Data on recruitment, growth and survival of individuals classified by size were gathered over 4 years.

3. Population growth rate (λ) was significantly higher in the unharvested meadow population than in control subplots of the outcrop population. Harvesting significantly reduced λ . Matrix model projections revealed that the size of outcrop populations would return to initial values within ≈ 5 years, only after 10% rhizome harvesting. In other treatments, recovery time varied from 17 (25% harvesting) to 33 (75%) years. In contrast, in the commercially harvested meadow population (with harvesting levels $>25\%$), projected recovery time was 6 years.

4. Higher growth rates and faster recovery in meadow populations appear to be due to higher recruitment and faster vegetative growth. In outcrops, slow growth and low fecundity slow down recovery after harvesting.

5. *Synthesis and application.* *Nardostachys grandiflora* is extremely sensitive to harvesting of rhizomes, but this sensitivity is higher in outcrop than in meadow habitats. Given the constraints on its population growth and its high sensitivity to harvesting, *N. grandiflora* should be strictly managed, with low harvest rates ($<10\%$ in outcrop and $<25\%$ in meadow) and fairly long rotations (at least 5 years) between successive harvests. This work shows the importance of considering demographic variation across habitats when formulating specific management plans for threatened medicinal plants. It also demonstrates the importance of integrating local harvesting practices in ecological research for informing management. A large proportion of high-altitude perennial medicinal plants may be expected to be similarly sensitive to exploitation, requiring careful management to achieve sustainable harvesting.

Key-words: conservation ecology, ethnoecology, Himalaya, medicinal plant conservation, Nepal, NTFP, population dynamics

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Introduction

In recent decades, the use of many plant-based, non-timber forest products (NTFPs), including medicinal plants, has gone from subsistence collection to large-scale commercial extraction, increasing the probability of overexploitation. Extraction of NTFPs affects survival, growth and reproduction of harvested individuals and thereby affects population structure and dynamics. Designing sustainable management of NTFPs requires information on the impact of harvesting on life-history parameters of focal species, knowledge of how populations of these species respond to different harvesting regimes, and estimation of harvest levels that will allow long-term persistence (Ticktin 2004). Management also requires understanding of local perceptions, knowledge and decision-making systems relating to resources. Here we focus on the impact of harvesting; a companion paper treats the perceptions and knowledge of local users (Ghimire, McKey & Aumeeruddy-Thomas 2004).

Matrix population models provide powerful tools for studying population dynamics of threatened plant species and applying results to sustainable management (Caswell 2001). This approach integrates the effects of management on life-history components (survival, growth, reproduction, mortality) and population dynamics (Kaye *et al.* 2001). Matrix models are increasingly being used to assess impacts of harvesting on life-history processes, identify optimal harvest regimes and suggest management measures for sustainable use of NTFP species. However, most demographic studies have focused on palms or other woody species; little is known about the long-term effects of harvesting on the demographic viability of herbaceous perennials (for review see Ticktin 2004). Demographic studies have shown that the impact of harvesting and patterns of postharvest recovery of NTFP populations can be influenced by characteristics of the harvesting regime (e.g. intensity, frequency, timing), characteristics of the affected plant species (e.g. life form, regeneration capabilities), plant parts harvested, and environmental conditions (reviewed by Ticktin 2004).

Sustainable harvesting of underground parts (rhizomes, roots, bulbs or other storage organs) of long-lived species presents a particular challenge. Long life spans allow populations to withstand long periods of unfavourable environmental conditions. However, if population numbers are reduced, recovery in long-lived species can be slow, because changes in demographic parameters strongly affect recruitment (Schemske *et al.* 1994; Raimondo & Donaldson 2003). Harvesting of underground parts of most herbaceous perennial species studied to date has been reported to be unsustainable, even at low levels (Nault & Gagnon 1993; Nantel, Gagnon & Nault 1996; Rock, Beckage & Gross 2004). Any levels of use found to be sustainable vary among species, depending on the ability of individuals to survive harvesting, recover from damage, and reproduce (Anderson & Rowney 1999). Population recovery in herbaceous perennial species after harvesting of roots or rhizomes has been shown to depend on several factors (e.g. resource availability) that stimulate (or inhibit) plant growth (Ticktin & Nantel 2004).

Here we address the sustainability of harvesting of a threatened perennial medicinal and aromatic herb of the Himalayas, *Nardostachys grandiflora* DC. (Valerianaceae) (hereafter referred to as *Nardostachys*), listed in Appendix II of CITES. *Nardostachys* is highly threatened, mainly due to overharvesting of its rhizomes for regional and international trade (Mulliken 2000). Despite its high conservation value, no detailed population ecological data are available from anywhere within its range (but see Ghimire, McKey & Aumeeruddy-Thomas 2005). We used matrix models to assess the effect on growth of *Nardostachys* populations of experimental harvesting of its underground rhizomes, applying local practices. We compared demographic variation in populations growing in rocky-outcrop and meadow habitats, and propose sustainable management strategies suggested by our results. The following questions are addressed: (1) Do populations in the two habitat types differ in structure and in rates of reproduction, survival and growth? (2) What are the consequences of harvesting for population growth in the two habitat types? (3) Which demographic processes are most important in producing the changes in growth rate caused by harvesting? (4) How do different harvesting regimes influence future population size?

Materials and methods

STUDY SPECIES

Nardostachys is a long-lived, rhizome-bearing perennial herb. Its small, highly aromatic rhizomes represent an important source of traditional medicine and incense. *Nardostachys* is found in high-altitude habitats (3500 to >5000 m) in the Himalayas, and grows in rocky slopes, rock outcrops, meadows, shrublands and forests. Its short growing season extends from May to early October. The plant's caespitose growth form corresponds to a 'phalanx strategy' (Lovett Doust 1981) of clonal growth, producing a dense clump, in which the successive ramets are compactly arranged and remain connected. Vegetative spread is usually slow and the fragmentation and independent existence of ramets is accidental and rare.

A single plant can have up to 21 ramets in a dense cluster. Each ramet is composed of two to 10 linear-lanceolate to oblanceolate leaves, and generally produces one, or in rare cases two to three, inflorescences in June–July. Flowers are scented and white, sometimes purpletinged, borne in umbellate heads. Flowers have very small gibbous (nectar containers); small insects such as flies are considered the probable pollinators (Eriksen 1989). An inflorescence can produce up to 25 achenes (hereafter referred to as seeds); they mature in August/September. Seeds are passively dispersed in late September by wind, water or gravity, and germinate by May/June of the following year. Seedlings grow into small rosettes during their first year. Their growth to reproductive size may take several years.

STUDY POPULATIONS AND SAMPLING DESIGN

The study area (29°05'–29°12' N, 82°40'–82°55' E) lies in Shey-Phoksundo National Park and its buffer zone in north-western Nepal. The area is characterized by trans-Himalayan ecology with low annual rainfall (450–800 mm). Local inhabitants are highly dependent on natural resources for their livelihood. Harvesting of medicinal plants is a major source of income in the buffer zone, providing up to 20% of total household income.

We identified study populations in collaboration with commercial harvesters, *amchi* (traditional medical practitioners trained in the Tibetan medical system) and national park staff, selecting two relatively less-disturbed populations inside the park, in rocky-outcrop and meadow habitats, respectively. These were located far (>6 km) from villages and receive low human pressure. Similarly, we selected one commercially exploited population, growing in meadow habitat, in the buffer zone (<4 km from the nearest village). We focused on populations growing in meadow and rocky habitats because plants growing in these habitats are locally perceived to have more value than those growing in other habitat types (forests and shrublands) because of their highly aromatic rhizomes (Ghimire *et al.* 2004). Studied populations lie above the tree line, at 3800–4200 m. In outcrops, soil had high pH (6.9–7.7), low moisture (18–28%), and low organic matter (2.5–6.5%) compared with meadows, in which these values ranged 4.9–5.5, 39–45% and 12–15%, respectively (S.K.G., unpublished data).

In the outcrop habitat we established three permanent plots, each 50–100 m apart. Each plot consisted of five parallel belt transects (5 × 1 m) spaced 1 m apart. Each transect was divided into five contiguous subplots (1 × 1 m). Thus in total we established 25 subplots in each plot. In meadows, we established two permanent plots, each consisting of three to four parallel belt transects (5 × 1 m), and similarly divided each transect into five 1-m² subplots.

An individual of *Nardostachys* was defined as all ramets connected into a dense clump (Damman & Cain 1998; Colling, Matthies & Reckinger 2002). Because of the plant's compact growth form, such individuals can be readily distinguished from each other with a high degree of certainty. In some doubtful cases, separation between adjacent individuals was verified by confirming the absence of underground connections. All such individuals initially present (10–15 individual clumps per subplot in 1998) and those that became established during successive censuses were mapped and permanently marked with small aluminium tags. Each ramet within each individual was also marked separately.

HARVESTING TREATMENT AND POPULATION MONITORING

In the Himalaya, users of *Nardostachys* can be broadly divided into three groups: (i) commercial collectors, who harvest on a large scale for trade; (ii) specialists in traditional medicine, who harvest for local healthcare purposes as well as for incense; and (iii) non-specialist local people, who harvest only for incense (Ghimire *et al.* 2004, 2005). In the present study, we applied the harvesting approach of *amchi* (one of the classes of specialist users) in our simulation experiment.

Harvesting treatments were applied only in the population from outcrop habitats located inside the park. An agreement was made with users that the plots located within the park would not be otherwise harvested or disturbed during the period of the study. The unprotected meadow plots located in the buffer zone were under more open access to commercial collectors. They therefore simply represent a situation of high harvest level. At the end of the growing season (September 1998), we asked the local *amchi* to apply harvesting treatments. Harvesting treatments were: removal of 0 (control), 10, 25, 50 and 75% of rhizomes from mature clumps (based on clone size, number of ramets, etc.). Harvesting followed their usual selective practices, with the exception that levels of simulated harvest above 10% exceeded those usually practised. *Amchi* are knowledgeable about the ecology and cultivation of medicinal plants, and their harvesting approach aims at sustaining regenera-

tion (Ghimire *et al.* 2004). Further details of the experiment are given by Ghimire *et al.* (2005). In each transect, each subplot was randomly assigned a different treatment. In total, each treatment received five replications per plot. Although the commercial harvester's approach was not experimentally simulated *in situ*, levels of harvest exceeding 25% and up to 75%, as in our experiment, represent the whole range of commercial harvesting pressure. Moreover, the comparison of unharvested and commercially harvested meadow populations also gives a clear picture of the impact of commercial harvesters.

The fates of tagged individuals were followed at monthly intervals (June–September) during 1999 and 2000, and thereafter annually during the peak growing period (June/July) until 2002. However, in the buffer zone, the commercially harvested population was monitored only for 2 years (1999–2000) because we could not maintain plot boundaries and tags due to human pressure. In each census we recorded the following data in each subplot: (i) number of seedlings and juveniles; (ii) size (number of interconnected ramets) and reproductive status (number of inflorescences) of each adult; (iii) mortality. Mortality of an adult occurred when all its interconnected ramets died. In every census, we carefully inspected the interconnections between ramets. This helped in identifying which ramet belonged to which plant.

SEED PRODUCTION AND SEEDLING RECRUITMENT

In October of each census, when seeds had matured, we measured the number of seeds produced per inflorescence from a random subset of 20–30 flowering individuals (selected from outside the subplots) in each of the outcrop and meadow populations. At the beginning of the growing season (May) we introduced viable seeds ($n = 100$) into each of the five 1 × 1 m subplots, located in similar habitat adjacent to the plots where the demographic study was conducted, and monitored seedling recruitment at fortnightly intervals until August. In each census, we counted the number of seedlings that had newly appeared at the soil surface. Seedling-recruitment experiments were conducted only in the outcrop and unharvested meadow populations. The data resulting from these experiments, along with the information on seed production, were used to estimate stage-specific fecundities, which were calculated by dividing the total number of inflorescences produced per stage class by the number of individuals of this stage, and then multiplying by the mean number of seeds per inflorescence and by the probability of seedling recruitment. We assumed equal seedling recruitment probability for seeds produced under different harvesting treatments in the outcrop population, and for seeds produced in the unharvested and commercially harvested meadow populations.

POPULATION DYNAMICS

We used stage-based population projection matrix models (Lefkovich 1965) to estimate demographic parameters. We combined plant size and state (seedling, juvenile, adult) to classify individuals of *Nardostachys* into six stage classes (Table 1). We used the number of interconnected ramets per individual as the main criterion to measure size of adults. For each population and treatment, we built annual transition matrices, based on June/July censuses, by recording the following demographic parameters (Table 1; for life cycle graph see Fig. S1 in Supplementary Material): (i) average number of seedlings produced per reproductive adult (F , fecundity); (ii) proportions of individuals that survived and remained in the same

Table 1. Stage classes and population projection matrix showing matrix elements (a_{ij}) with possible transition probabilities between stages from one year (t , columns) to the next ($t + 1$, rows)

Stage	Explanation	Sd	J	A1	A2	A3	A4
Seedling (Sd)	Seedling with cotyledon leaves	–	–	F ₁₃	F ₁₄	F ₁₅	F ₁₆
Juvenile (J)	Small plant with one ramet	P ₂₁	S ₂₂	–	–	–	–
Adult 1 (A1)	Adult with 1–3 ramets	P ₃₁	P ₃₂	S ₃₃	R ₃₄	R ₃₅	R ₃₆
Adult 2 (A2)	Adult with 4–6 ramets	P ₄₁	P ₄₂	P ₄₃	S ₄₄	R ₄₅	R ₄₆
Adult 3 (A3)	Adult with 7–9 ramets	–	P ₅₂	P ₅₃	P ₅₄	S ₅₅	R ₅₆
Adult 4 (A4)	Adult with ≥10 ramets	–	–	P ₆₃	P ₆₄	P ₆₅	S ₆₆

Matrix elements assigned to stasis (S), progression (P), retrogression (R) and fecundity (F).

size class (S, stasis); (iii) proportions that survived and grew to a larger size class (P, progression); and (iv) proportions that survived but shrank into a smaller size class (R, retrogression). We also built a set of average matrices, one for each treatment in the outcrop population and one for the unharvested meadow population. Each average matrix was a weighted mean of the three annual matrices, built by weighting each transition within a column by the sample size. We analysed each transition matrix to calculate the asymptotic population growth rate (λ) and stable size distribution (Caswell 2001), and compared those quantities between habitats and among treatments. The 95% confidence intervals (CI) of the λ value of each annual transition matrix were estimated by the bootstrap percentile-interval method (Caswell 2001). Differences between observed and stable stage distributions were assessed by Keyfitz's dissimilarity index (Δ , Keyfitz 1968). We performed stochastic and deterministic simulations of transition matrices to estimate extinction probabilities, transient dynamics and postharvest population recovery time. See Appendix S1 for further details.

We performed elasticity analyses to assess the relative contribution of each matrix element to λ (Caswell 2001). More specifically, we studied the overall effect of proportional changes in sets of transitions, representing four demographic processes (stasis, progression, retrogression and sexual fecundity) and the six stage categories. We used life table response experiment (LTRE, Caswell 2001) analysis to quantify the contribution of each transition to the observed variation in λ between habitats and among treatments (see Appendix S1 for further details).

Matrix model analyses were performed in MATLAB ver. 5.3 (Math Works, Inc., Novi, MI, USA) and using the program DÉMOGRAPHE (Nantel 2004). Population structure and reproductive data were analysed using statistical tests in SPSS ver. 11.5. We used parametric tests when data met the necessary conditions; non-parametric tests were conducted in other cases. Differences in flowering frequency and plant survival between habitats and among treatments were determined by goodness-of-fit tests. Rate of seed production and seedling recruitment in different habitats were compared using either Mann–Whitney U -tests or one-way ANOVA.

Results

STAGE STRUCTURE AND REPRODUCTION

We first compared population stage structure and reproduction between the unharvested meadow population and control subplots (0% harvesting) in the outcrop population, and then assessed the effect of harvesting on these parameters. We found significant differences in the observed stage distribution

between these two populations (Kolmogorov–Smirnov $Z = 9.63$, $P < 0.001$; Table 2). The meadow population had higher proportions of plants in smaller size classes than did the outcrop population. However, in both populations observed stage distributions did not differ much from the estimated stable stage distribution, as shown by small values of Keyfitz's Δ (Table 2).

The meadow population had a higher frequency of flowering adults than the outcrop population ($\chi^2 = 144.74$, $P < 0.0001$; Table 3). There was a positive relationship between number of ramets and a genet's probability of flowering (logistic regression: Wald statistic = 11.62, odds ratio 1.92, $df = 1$, $P = 0.001$). Thus, among adults, larger plants had a higher probability of flowering than those in smaller size classes. Although the two populations showed differences in flowering frequency, seed set per inflorescence did not differ significantly between them (Mann–Whitney $U = 3132.5$, $n = 159$, $P = 0.817$; Table 3). However, seeds produced in the meadow population were significantly heavier than seeds produced in the outcrop population (ANOVA, $F_{1,85} = 60.68$, $P < 0.0001$).

Under field conditions, seedling recruitment was low in both populations, but overall recruitment rate was higher in the meadow (mean \pm SD, $16.4 \pm 5.7\%$) than in the outcrop population ($4.7 \pm 3.3\%$) ($F_{1,24} = 49.68$, $P = 0.0001$; Table 3). There were no significant differences in seedling recruitment among years. As a result of higher flowering frequency and seedling recruitment rate in the unharvested meadow population, fecundity was higher in this population than in control subplots of the outcrop population. In both populations, fecundity increased from stage A1 to A4 (Table S1).

The observed stage distributions in the commercially harvested meadow population and in the outcrop population subjected to different harvesting treatments were dramatically different from stable stage distributions that are expected without harvest, as indicated by large values of Keyfitz's Δ (Table 2). In the outcrop population, as harvesting treatments involved selective removal of rhizomes from individuals of large size classes, many of the differences between observed and stable stage distributions were found in adult stages (A1–A4). While proportions of large adults (A3 and A4) were reduced, proportions of smaller adults (A1 and A2) increased. Reduction in the proportion of large adults among treatments had a marked influence on flowering probability ($\chi^2 = 115.32$, $P < 0.0001$; Fig. 1) and thus on fecundity among treatments

Table 2. Observed (Ob) and simulated stable stage (St) distributions for different 1-year periods and for different harvesting treatments and populations

Stage class*	Outcrop \longrightarrow						Meadow† \longrightarrow		
	Ob-0% Control	St-0% Control	Ob-10%	Ob-25%	Ob-50%	Ob-75%	Ob-UH	St-UH	Ob-CH
1999–2000									
Sd	0.060	0.060	0.077	0.080	0.097	0.086	0.253	0.200	0.095
J	0.041	0.029	0.111	0.115	0.103	0.108	0.185	0.093	0.081
A1	0.207	0.095	0.101	0.184	0.245	0.338	0.164	0.151	0.054
A2	0.230	0.151	0.275	0.316	0.245	0.237	0.171	0.190	0.203
A3	0.152	0.275	0.198	0.161	0.135	0.129	0.130	0.165	0.405
A4	0.309	0.389	0.237	0.144	0.174	0.101	0.096	0.200	0.162
Keyfitz's Δ ‡		0.204	0.229	0.359	0.345	0.434		0.159	0.252
2000–01									
Sd	0.060	0.040	0.077	0.145	0.160	0.121	0.217	0.260	–
J	0.032	0.012	0.036	0.044	0.053	0.047	0.120	0.112	–
A1	0.147	0.089	0.267	0.358	0.473	0.607	0.199	0.247	–
A2	0.198	0.203	0.277	0.321	0.214	0.131	0.211	0.159	–
A3	0.244	0.305	0.169	0.063	0.038	0.056	0.127	0.134	–
A4	0.318	0.350	0.174	0.069	0.061	0.037	0.127	0.087	–
Keyfitz's Δ		0.098	0.312	0.523	0.556	0.634		0.100	–
2001–02									
Sd	0.088	0.128	0.070	0.128	0.128	0.118	0.184	0.266	–
J	0.018	0.055	0.032	0.061	0.094	0.047	0.106	0.123	–
A1	0.123	0.123	0.203	0.331	0.393	0.553	0.251	0.214	–
A2	0.216	0.187	0.326	0.311	0.248	0.188	0.179	0.157	–
A3	0.256	0.206	0.219	0.101	0.094	0.047	0.168	0.164	–
A4	0.300	0.301	0.150	0.068	0.043	0.047	0.112	0.077	–
Keyfitz's Δ		0.079	0.233	0.337	0.370	0.430		0.098	–

*For stage class see Table 1.

†UH, unharvested meadow population; CH, commercially harvested meadow population.

‡Keyfitz's Δ is a standard measure of the distance between probability vectors (Caswell 2001). Its values range between 0 (when the vectors are identical) to 1 (when the vectors are different).

Table 3. Reproductive characteristics of the unharvested meadow population and of control subplots of the outcrop population (mean \pm SD)

Parameter	Outcrop			Meadow		
	1999	2000	2001	1999	2000	2001
Flowering frequency (%)*	25.64	22.84	17.56	51.16	39.62	30.65
Seed set per inflorescence	3.0 \pm 2.4	3.1 \pm 2.7	9.4 \pm 6.7	1.9 \pm 2.3	6.2 \pm 5.4	7.7 \pm 5.8
Seed mass (mg)	–	2.1 \pm 0.5	2.5 \pm 0.3	–	3.1 \pm 1.0	3.9 \pm 0.8
<i>In situ</i> seedling recruitment (%)	5.0 \pm 5.1	3.8 \pm 2.6	5.4 \pm 1.9	16.4 \pm 4.5	13.2 \pm 3.3	19.6 \pm 7.4

*Only individuals in adult stage classes were included.

(Table S1). The probability of flowering was comparatively low in individuals whose size had been reduced by harvesting (for example, flowering frequency was higher in unharvested A2 or A3 individuals than in A2 or A3 individuals resulting from harvesting of A4 or A3 individuals). However, 10% harvesting, which is typical of the *amchi* practices, did not significantly reduce flowering probability ($\chi^2 = 3.03$, $P = 0.082$).

SURVIVAL AND GROWTH

Survival was strongly size-dependent in both populations. In unharvested subplots, adult plants rarely died over the study

period (Table S2). In both populations, survival of adults (A1–A4) in unharvested subplots varied from 88 to 100%. Survival was lowest for seedlings (S, 46–78%) and intermediate for juveniles (J, 68–90%). However, survival of seedlings was higher in the unharvested meadow population (61–78%) than in unharvested subplots of the outcrop population (46–55%) across the 3 years. Harvesting of rhizomes led to increased mortality of adults remaining after harvest (Table S2), but the result was significant only for the first transition year ($\chi^2 = 110.4$, $P < 0.0001$). Adults from which some rhizomes were harvested, and unharvested individuals that were in close proximity to these harvested individuals, accounted for this

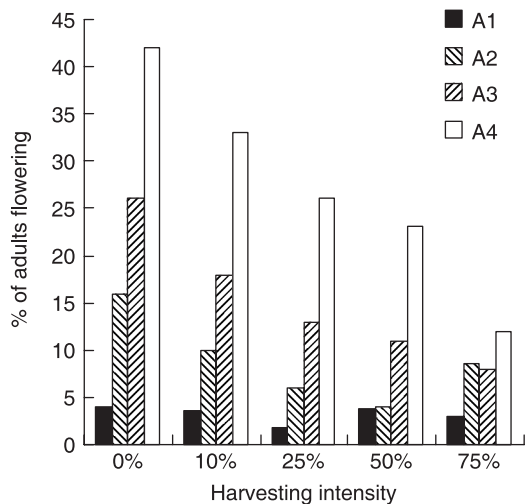


Fig. 1. Effects of harvesting on flowering: overall percentage (mean of 1999–2002) of adults (A1–A4) that flowered in different harvesting treatments in the outcrop population.

increased mortality. The death of adults in close proximity to harvested individuals was due to the effect of trampling, and to a marked effect of harvesting on stability of soils on the steep slopes of rocky outcrops. In the commercially harvested population, even higher mortality of plants remaining after harvest was observed than in simulation plots in the rocky-outcrop population. Vegetative growth, measured as the number of interconnected ramets per individual, tended to be higher in control subplots of the outcrop population (mean \pm SD over 1999–2002, 6.58 ± 3.43 ; range 1–21) than in the unharvested meadow population (4.58 ± 3.20 ; range 1–17).

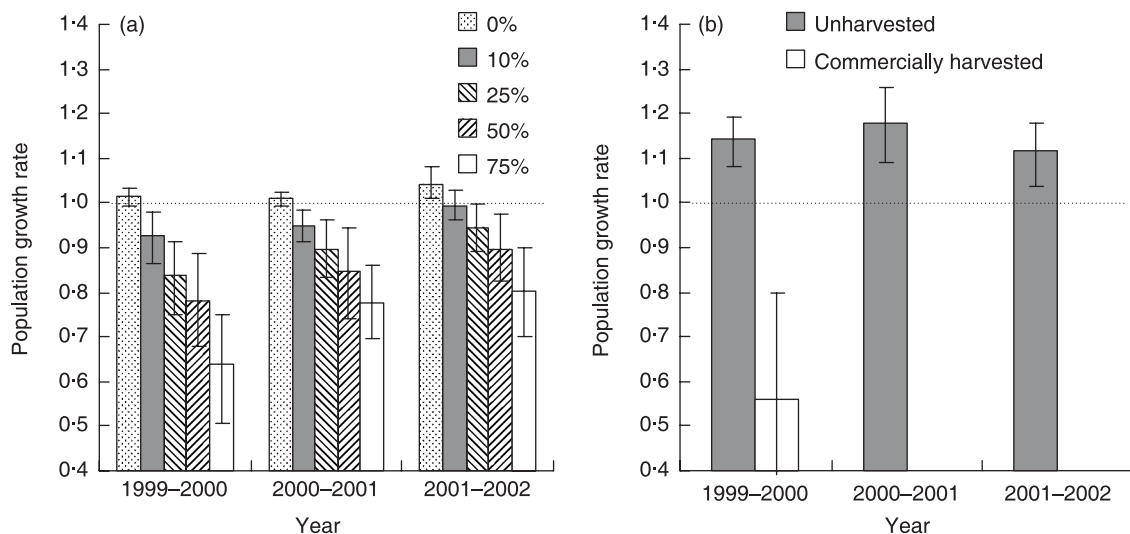


Fig. 2. Asymptotic population growth rates (λ) and 95% CI for (a) each harvesting treatment and year in the outcrop population; (b) unharvested and commercially harvested meadow populations. For the commercially harvested meadow population, the λ value shown is for 1999–2000.

POPULATION GROWTH RATES

Asymptotic population growth rates (λ) were higher in the unharvested meadow population (1.12–1.17) than in control subplots of the outcrop population (1.01–1.04) in all study years (Fig. 2). For the first two transition years (1999–2000, 2000–01), λ values of these two populations had non-overlapping 95% CI, indicating significant differences. For the unharvested meadow population, all the matrix models predicted λ significantly >1 . For the outcrop population, predicted λ was significantly >1 only in the year 2001–02; in other years λ values were not significantly different from 1 (Fig. 2).

Harvesting reduced λ in both habitat types (Fig. 2). For subplots in the outcrop population subjected to experimental harvesting, the predicted λ values for 1999–2000 were 0.637, 0.779, 0.838 and 0.928 under 75, 50, 25 and 10% harvesting, respectively (Fig. 2a). All these differed significantly from the predicted value for the control subplots (1.014), based on non-overlapping 95% CI. In 2000–01 and 2001–02, λ values gradually increased in all treatments. However, in all cases λ values of harvested subplots were significantly lower than those of control subplots, except for the 10% harvest level.

ELASTICITY ANALYSES

In control subplots of the outcrop population, the probability of stasis (S, survival and remaining in the same stage) generally made the largest contributions to λ (Fig. 3). In the unharvested meadow population, progression (P, growing to a larger size class or vegetative growth) contributed more to λ than did stasis. Similarly, fecundity (F) contributed more to λ in the meadow than in control subplots of the outcrop population. The highest elasticity values were due to contributions of individuals from large size classes. However, the contribution of seedlings and juveniles to λ in the meadow population was

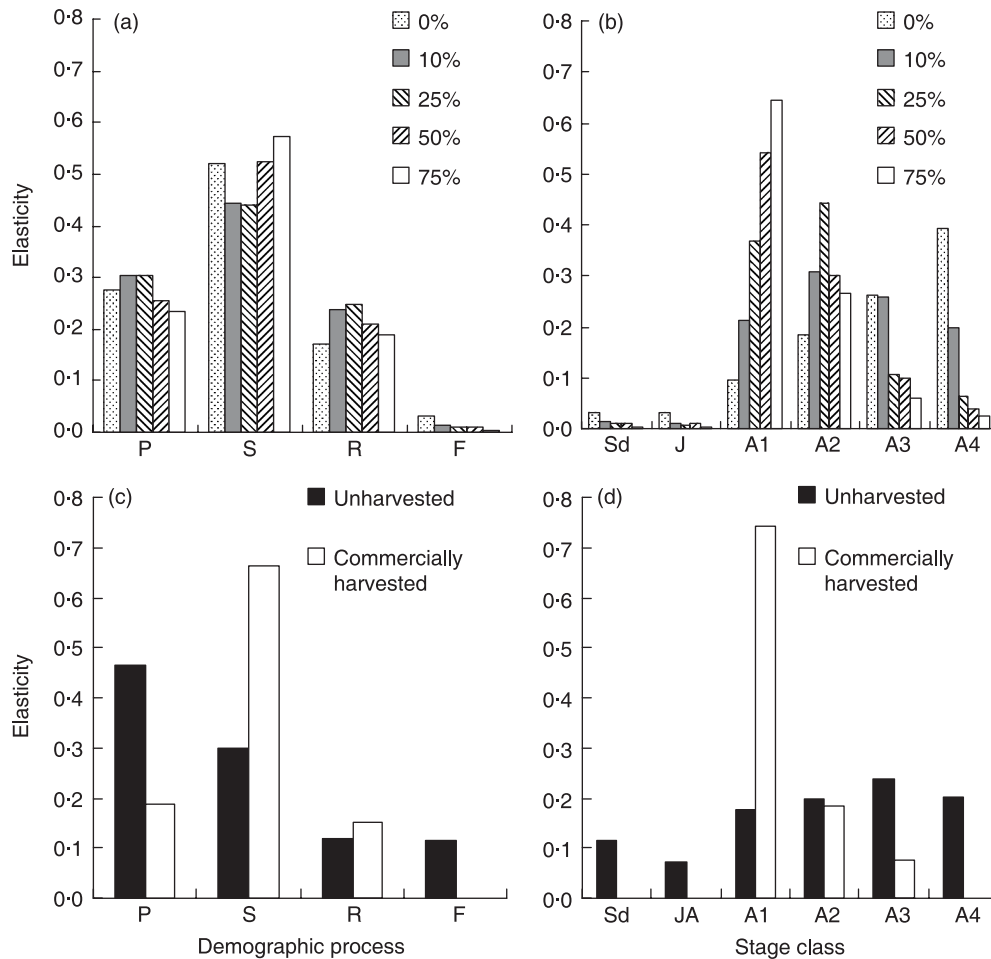


Fig. 3. Sum of elasticity values for four demographic processes (progression, stasis, retrogression and fecundity) and for six stages (seedling, juvenile and adult 1–4). Elasticity values for (a,b) the outcrop population subjected to different harvesting treatments; (c,d) the unharvested and commercially harvested meadow populations. Elasticity values were calculated from weighted average matrices, except for the commercially harvested population, in which elasticity values were for the year 1999–2000. For stage classes see Table 1.

almost double their contribution in the outcrop population. In the latter, as harvesting intensity increased, survival of adults of progressively smaller size classes made a greater contribution to λ . This was mainly due to the fact that selective harvesting involved removal of rhizomes from individuals of larger size classes. Of the vital rates considered, fecundity had the lowest influence on changes in λ in all treatments.

LIFE-TABLE RESPONSE EXPERIMENT ANALYSIS

The LTRE analysis showed that harvesting in the outcrop population affected population growth mainly through effects on progression (vegetative growth) and stasis, while fecundity made smaller contributions (Fig. 4a). The contributions of progression, stasis and fecundity were negative, indicating that those probabilities declined following harvesting. The largest negative contributions were those of progression and of stasis at the highest harvest levels. The contributions of retrogression were positive, indicating higher shrinkage rates with

harvesting. LTRE further showed large differences in vital rates and in their contributions to growth rate between the unharvested meadow population and control subplots of the outcrop population (Fig. 4b). Only the contribution of stasis was positive, indicating that the probability of individuals remaining at the same stage was higher in the outcrop population. Contributions of fecundity, progression and retrogression were negative, indicating their greater effect on population growth rate in the meadow population.

TRANSIENT DYNAMICS, STOCHASTIC SIMULATIONS AND POPULATION RECOVERY

The analysis of transient dynamics (Fig. 5) indicated that the outcrop population (if subjected to harvest levels >25%) would have a high probability of extinction within 15 years if harvested annually at the rates of harvest applied in the first year. Even at 10% harvest levels, a rapid decline in population size was projected. The commercially harvested meadow population

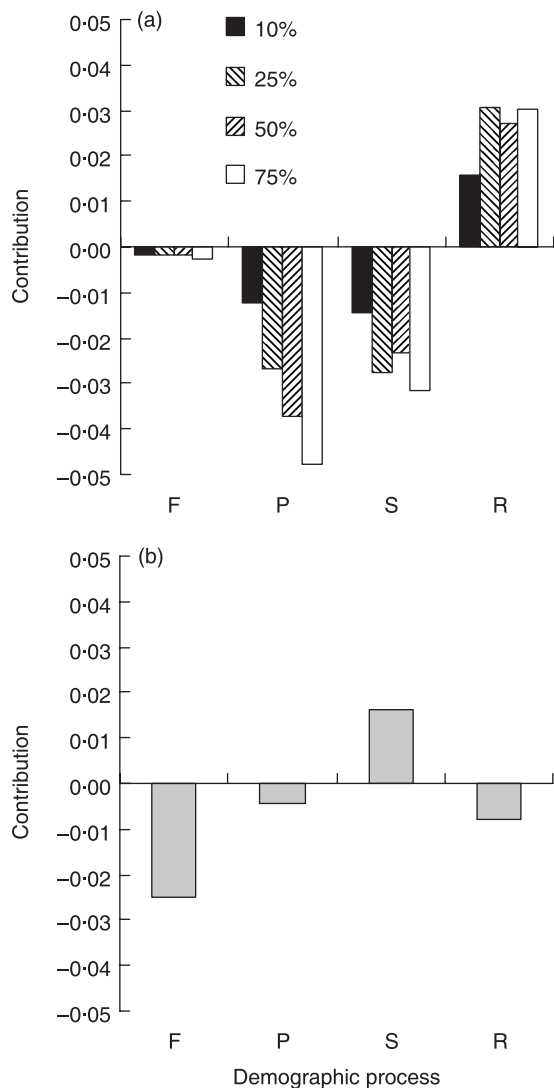


Fig. 4. Results of life table response experiment (LTRE) analysis based on weighted average matrices. (a) LTRE analysis for the outcrop population showing contributions of the four different demographic processes (abbreviations as in Fig. 3) to differences in population growth rate in different harvesting treatments relative to control. (b) LTRE analysis showing contributions of different demographic processes to differences in population growth rate between control subplots (0% harvesting) of the outcrop population and the unharvested meadow population; comparisons were made relative to the meadow population, so that greater negative values correspond to higher contribution of the process concerned in the meadow population.

(with harvesting levels >25%) showed an even more rapid rate of decline in population size. If left unharvested, the outcrop population would increase in size very slowly, whereas in the unharvested meadow, population size would increase more rapidly throughout the projected period.

Population growth rates calculated from stochastic simulations were very similar to those obtained from time-invariant deterministic projections (Table S1). Stochastic models showed that, without harvesting, both outcrop and meadow populations would have an extremely low probability

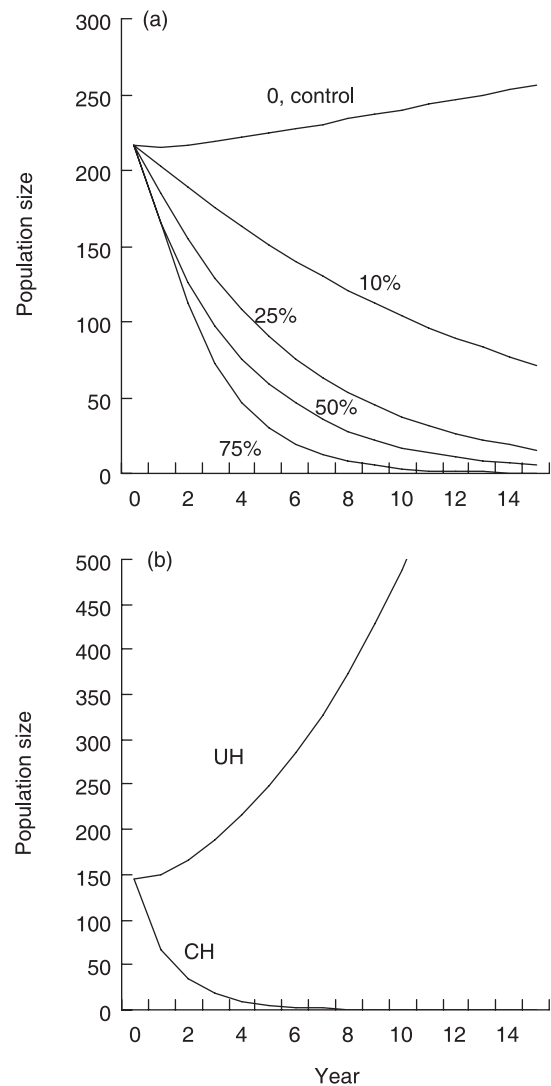


Fig. 5. Transient dynamics of *Nardostachys grandiflora* populations based on 1999–2000 transition matrices. Projection of population size for 15 years (a) in different harvesting treatments in the outcrop population; (b) in the unharvested (UH) and commercially harvested (CH) meadow populations. Initial population structures were those of control plots for the outcrop population ($n = 220$) and those of the unharvested meadow population ($n = 146$).

of extinction within 100 years. In our stochastic simulation, in none of the 1000 runs (each 100 years) did an unharvested population go to extinction in either habitat. However, extinction probability was non-negligible even at the lowest level of harvesting. The probabilities of extinction for 10, 25, 50 and 75% harvest levels were 0.14, 0.68, 0.77 and 0.87, respectively.

Deterministic projection of transition matrices revealed that when rhizomes are selectively harvested, only once, at the rate of 10%, the outcrop population would return to its initial size after 5 years of harvesting. In other treatments, recovery time varied from 17 years (25% harvesting) to 33 years (75%). In contrast, in the commercially harvested meadow population, projected recovery time was 6 years.

Discussion

Opportunities for experimental work on rare and threatened species are generally constrained because proper replication is usually difficult to achieve. However, the challenges imposed by highly threatened species must be met if their conservation is to be achieved. Our comparison of the response of *Nardostachys* to harvesting and effect of habitat was based on replicates within a single population in each of the two habitats; further replication was logistically impossible. Despite these limitations, our work has provided clear insights into how habitat variation and harvesting affect demographic processes and population dynamics in *Nardostachys*.

DEMOGRAPHY

Meadow and outcrop populations had significantly different observed stage structures. While large adults comprised a high proportion of individuals in the outcrop population, the meadow population showed higher proportions of individuals in smaller size classes. Proportions of seedlings and juveniles were much lower in the outcrop population. Large adults are frequently numerically dominant in populations of perennial species with clonal growth (Cook 1985), and seedling recruitment is often greatly reduced in populations growing in harsh environments (Baskin & Baskin 1998). Habitat-specific variation in germination traits is common in perennial subalpine and alpine herbs and is often related to spatiotemporal patterns of seed availability, snowmelt time and availability of safe sites for germination (Shimono & Kudo 2003).

We found strong size-dependence of fecundity and survival in both populations, in accordance with other studies (Drechsler *et al.* 1999; Méndez & Karlsson 2004). The higher fecundity in the meadow population was due to higher flowering frequency and higher rate of seedling recruitment than in the outcrop population. Although sexual fecundity was lower in the outcrop population, number of ramets per individual was higher than in the meadow population. Thus outcrop plants tended to invest less in sexual fecundity and more in traits ensuring persistence of vegetative offshoots (or production of new ones, although this seems to be very slow in this harsh environment). Long-lived species that invest more in persistence or ability to resprout tend to have fewer seeds or seedlings and slower growth than non-sprouting species (Drechsler *et al.* 1999; Bond & Midgley 2001). Mortality was highest for seedlings and juveniles, particularly in the outcrop population, and lowest for the larger adults. The shallow root systems of seedlings and the stony substrate of outcrop habitats, where soil moisture and nutrient levels fluctuate considerably, may explain why seedling mortality relative to that of mature plants was even higher here than in meadow habitats. The short growing period in alpine environments is an additional factor affecting seedling establishment: only seedlings that attain a critical size by the end of the first growing season have a high probability of survival over winter (Shimono & Kudo 2003).

POPULATION GROWTH RATES

Growth rates of the meadow population were significantly >1 , indicating positive growth of the population in the absence of disturbance. In contrast, growth rates in the outcrop population were not significantly >1 in two out of three transition years, indicating very slow population growth. In both habitats, population growth rates did not differ much among years. Other studies have also reported low variation of population growth rate among years, but high variation among habitats (Menges & Dolan 1998). As deterministic models alone do not provide accurate estimations of population growth rates, we also ran stochastic simulations to incorporate environmental variation. Stochastic simulation of matrices for a 100-year period showed that, without harvesting, both populations have an extremely low probability of extinction. However, extinction probability was non-negligible even at the lowest level of harvesting (0.14 at 10% harvesting). Uncertainty in parameter estimates may lead to bias in assessment of extinction time (Taylor 1995). Still, rates of population growth predicted by a deterministic model of weighted average matrices and by our stochastic model were very similar (Table S1).

Elasticity analysis showed that progression (vegetative growth) had the highest functional contribution to asymptotic population growth rate in the meadow population, followed by stasis and fecundity. Fecundity had a much lower contribution to population growth rate in the outcrop population. This study shows that the large-adult stage, by its capacity for vegetative growth or at least for stasis, represents a critical life-history stage that strongly influences growth rate of the outcrop population. High adult survival rate and tendency of adults to remain at the same size (stasis) also characterize other perennial species (Silvertown *et al.* 1993; Silvertown, Franco & Menges 1996). Such trade-offs between stasis and population growth and between persistence and fecundity have implications for population management (cf. Raimondo & Donaldson 2003). In slow-growing, long-lived species with persistent, resprouting life histories, low recruitment and low fecundity slow down population recovery after harvesting (Raimondo & Donaldson 2003). However, some faster-growing herbaceous species achieve rapid recovery after harvest through vegetative propagation (Ticktin & Nantel 2004). In our case, plants growing in outcrop habitat showed slow growth and low level of recovery despite their capacity for vegetative propagation.

The LTRE analysis clearly showed that, while the outcrop population was more static, the meadow population was very dynamic, with all demographic processes contributing greatly to change in population size. The main reasons for higher growth rates in the meadow population appear to be the greater rate of sexual reproduction and faster individual growth (production of ramets). Differential patterns of ramet recruitment and growth in different habitats also underlie variation in population growth rates in other perennial herbs (Ticktin & Nantel 2004). Plastic responses to environmental factors such as light and nutrient availabilities are a major cause of intraspecific variation in clonal traits (Birch & Hutchings 1994).

Although the overall number of ramets per individual was higher in the outcrop population than in the meadow population, production (accumulation) of such ramets seems to be a very slow process in the outcrop population. In a greenhouse experiment, we found that in their first year of growth, transplanted seedlings from the meadow population ($n = 60$) produced an average of 3.2 ± 1.4 (range 0–6) daughter ramets, but none of the transplanted seedlings ($n = 60$) from the outcrop population produced daughter ramets within a year when grown under the same conditions (S.K.G., unpublished data). This suggests not only a direct effect of environment, but also genetic or maternal effects.

EFFECT OF HARVESTING

Harvesting of underground plant parts can have important effects on plant population dynamics (Rock *et al.* 2004). We found that harvesting of rhizomes affected most aspects of the demography of *Nardostachys*. Harvesting had marked influences on fecundity and growth of large individuals; it also significantly reduced population growth rate, and the effect increased with harvest intensity. While population growth rates tended to increase over the study period, at all harvesting levels λ was still < 1 at the end of the study. The slow growth and low fecundity of *Nardostachys* thus slows its recovery after harvesting. At high harvest intensity, the survival of small and medium-sized adults (A1–A2) is particularly important in permitting recovery. The LTRE analysis clearly showed that the largest negative contributions to population growth rates at high harvest levels arose from effects of harvest on growth and survival.

CONSERVATION OF *NARDOSTACHYS*

Severe overharvesting of *Nardostachys* throughout the Himalayas has jeopardized many natural populations, motivating a variety of experiments, such as enrichment planting in community forests (Aumeeruddy-Thomas *et al.* 2005). Understanding the response of plants and populations to harvesting is a key ingredient in the success of these experiments.

The effect of harvesting on a population depends on its frequency and intensity, environmental conditions, and the capacity of individuals to survive and reproduce after harvest (Ticktin 2004). Our results suggest that sustainable harvest of *Nardostachys* is possible only at very low harvest intensity with long rotations. However, environmental variation appears to affect how rapidly populations can recover from the loss of individuals. Differences in growth rates in different habitats can have important conservation and socio-economic implications (Ticktin & Nantel 2004). Our deterministic projection revealed that, in outcrop populations, harvesting could be sustainable if $< 10\%$ of rhizomes are removed at intervals of at least 5 years, whereas in meadow populations slightly higher harvesting rates (up to 25%) could be sustained, as recovery after harvest is projected to be faster in these populations.

The harvesting approaches applied in our experiment were those of *amchi*, specialists trained in Tibetan medicine. *Amchi* harvest small amounts of *Nardostachys* (≈ 6.0 kg per *amchi* per

year, with harvest rates that usually do not exceed 10%). They are highly selective, harvesting mature parts from selected populations during a specific period (at the end of the growing season in the case of *Nardostachys*). Their selective harvesting approach depends on their overall perception of the ecology and regeneration potential of plants. Thus they leave individuals of immature size classes, which will then have an opportunity to grow and can be harvested in the future. In everyday life, they monitor the vigour of harvested populations and make decisions to shift to other harvesting sites if necessary. Additional management approaches adopted by *amchi* include: (i) social regulations that control access to harvest sites to a certain extent; (ii) social and cultural rules limiting harvest to specific periods; (iii) transplanting of ramets *in situ* and cultivation in home gardens; and (iv) rotational grazing of livestock (for details see Ghimire *et al.* 2004). The level of rhizome harvesting simulated for *Nardostachys* in the outcrop population is well within the levels of practice of these specialist users (10% harvesting). Harvesting by commercial collectors, on the other hand, depends not on size and maturity of the plant, but on the response of collectors to market demand and value of the species (Ghimire *et al.* 2004, 2005). It is important to note that commercial harvesting of rhizomes in outcrop populations would lead to their rapid extinction. This would be an important loss both socially and biologically because the plants appear to have evolved specific adaptations to such alpine habitats. Interestingly, these populations are preferred by *amchi* because the plants have a higher medicinal potency. While meadow populations are more resilient, continuous application of high rates of commercial harvesting would nevertheless lead to a rapid decrease in population size.

Our results have shown that *Nardostachys* is extremely sensitive to harvesting of rhizomes. This sensitivity is attributed to its low rates of recruitment, high seedling and juvenile mortality, and higher rate of shrinkage from larger to smaller size classes when harvested. Given the limitations to its population growth and its high sensitivity to harvesting, *Nardostachys* should be strictly managed, with fairly long rotations between successive harvests. Given long recovery times and high vulnerability of populations to the loss of adults, it is vital that small, fragmented populations, particularly those growing in outcrops, be used only at strictly controlled rates for local healthcare needs. Continued monitoring by both biologists and local specialists such as *amchi* is also recommended for the long-term conservation management of this species.

Given the high harvesting pressure on this species, its cultivation and *in situ* enrichment planting should also be promoted. The *amchi*, with their acute knowledge of plants gained from observation and experiment, could be key partners in such endeavours. Precise management plans for medicinal plants based on their demographic response to harvesting across habitats are a key ingredient of a strategy for conservation that would integrate not only ecological and social factors, but also economic factors, for example through improvement of market circuits, thereby enabling local collectors to reap economic benefits from sustainable levels of harvesting (Aumeeruddy-Thomas *et al.* 2005).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Assessment of population dynamics of *Nardostachys grandiflora* using matrix modelling.

Fig. S1. Life-cycle graph of *Nardostachys grandiflora*.

Table S1. Effects of harvesting on matrix elements and on population growth rates of *Nardostachys grandiflora*

Table S2. Effects of harvesting and habitat on survival of *Nardostachys grandiflora*

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