Metapopulation modelling of threatened plants to assess conservation status and determine minimum viable population size

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Use of metapopulation modelling in conservation of threatened plants has been demonstrated in this article taking *Paris polyphylla* Smith as an example. The metapopulation data collected from Sikkim Himalaya over a period of four years were analysed using RAMAS Metapop 5.0 software. Demographic projection, assessment of extinction probability, population viability analysis, and analysis of impact of disturbance on the metapopulation were undertaken. The metapopulation had 11 populations of which seven were in continuous forest (CF) and four were in forest fragments (FF). All the analyses were done in two model scenarios, viz. base-model (M1) representing the disturbed condition, and alternate model (M2) representing the undisturbed condition for three distinct layers of *P. polyphylla* populations, i.e. CF, FF in isolation, and collectively as metapopulation. The outputs of the deterministic population models in respect of CF and FF populations revealed that both the populations had contribution of growth and survival of plants to such decline was greater than the fecundity in both the models. Stochastic simulations revealed an extinction risk of >10% in 100 years in M1 scenario, which put the species under vulnerable category. The extinction risk of metapopulation significantly varied between the two models (M1 = 0.85; M2 = 0.42), conforming the hypothesis that disturbance and forest fragmentation have detrimental effect on the persistence of *P. polyphylla*. Recovery of species was most promising when reproductive individuals were introduced to the M2 model. Thus, both introduction of individuals in the field and protection of the populations with emphasis on the reproductive subset would result in achieving minimum viable population size or low threat status of the species.

Keywords: Demography, extinction risk, metapopulation, minimum viable population.

Introduction

METAPOPULATION modelling is one of the most prospective tools in conservation biology. The primary goal of the present-day metapopulation modelling is population viability analysis (PVA) for assessing the current state of species populations in a given landscape. Besides using time-series data, prediction of future risk and exploration of management options are the two other outcomes. With advancement in technology, accuracy and reliability of simulation models have increased manifold. Brook *et al.*[1,2] tested the predictive capability of PVA software using long-term empirical data and concluded that the risk of population decline matched with observed outcome, and projections did not differ significantly from reality.

Spatially explicit models are useful in long-term studies where time series data are obtained on patch dynamics and population persistency. However, in short-term studies, metapopulation models that employ demographic parameters form an important basis of PVA. Inclusion of data on demographic processes that regulate the rate of growth or decline in population size makes the metapopulation models robust. Besides, integration of schedules of fecundity, recruitment and survival parameters into the models allows exploration of the relative importance of these parameters in meta-population dynamics[3,4]. Thus demography-based metapopulation models help us in understanding the mechanisms that govern population dynamics and also in estimating extinction probabilities[5,6].

A key measure of metapopulation modelling and PVA is determination of minimum viable population (MVP) size[7,8]. It is the threshold size that gives 95% probability of survival of a population over a 100-year period[9]. During the past three decades, MVP has been estimated for more than 200 species, of which only 23 are plants[10]. Significantly less work on PVA of plant species is due to the complexity of life-form, growth behaviour and spatial dynamics which make data collection task extremely challenging. Considering the outputs of metapopulation models, viz. projected demographic parameters and extinction probability, which are important for designing conservation actions, the utility of PVA tool in conservation planning for threatened plants has been demonstrated in this article.

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Paris polyphylla Smith (family Trilliaceae) is a vulnerable species distributed along the Eastern Himalayan range, including Nepal, Bhutan, parts of China and North East India. The species is threatened due to overexploitation for medicinal purposes. For its conservation planning, metapopulation modelling approach was applied. The present work is based on a demographic study conducted in the Sikkim Himalaya where the species thrives in small pockets in the temperate forest at an elevation range of 2500–3600 m amsl. The occurrence of the populations starts from the buffer zone of Khangchendzonga Biosphere Reserve (KBR) and continues up to the core zone, i.e. Khangchendzonga National Park, which is one of the 34 World Heritage sites of India[11].

Materials and methods

P. polyphylla is a polycarpic perennial plant with a short and thick rhizome bearing several irregular constrictions which are formed annually due to formation of annual shoots. Seedling emergence takes place during spring about a month after the emergence of stem from perennating rhizome. Germinated seeds show rapid growth of radicle that forms the rhizome system, followed by plumule and stem elongation. Growth of seedling is slow and they do not reproduce in the first year. Upper shoots wither early before the onset of winter and the plant survives as dormant rhizome during winter. Older plants flower early during June–July and set fruits during August–early October. The plant produces a single berry which contains 20–50 seeds.

The metapopulation of *P. polyphylla* in the Sikkim Himalaya occurred in a forest with various intersects of trekking paths, grazing and human disturbances. A total of 11 populations were identified and studied in the KBR (Table 1), out of which seven were in continuous forest (CF) habitat and four were in isolated forest fragments (FF).

Data structure and analysis

Three demographic stages, viz. seedling, adult and reproductive individuals were distinguished in the life history of *P. polyphylla*.

(i) *Seedlings*: Individuals that developed from germinated seeds consisting of 2–4 leaves with a short stem of 4–10 cm length.

(ii) *Adults*: Seedlings reached adult stage after at least one year of emergence. The stage was characterized by the size of leaves and height of stem.

(iii) *Reproductive*: Individuals were similar in size to those of adult stage, but differed in the development of inflorescence at the apex of the leaf whorl.

Demographic data were collected over a period of four years for each of the identified populations. Based on analysis of soil and micro-environmental attributes, habitat similarity among the populations of CF and FF was established. The demographic data were prepared into two sets representing CF and FF populations and their corresponding transition matrices were computed for model projection.

The analysis was done in two different scenarios, viz. base model (M1) representing the disturbed condition and alternate model (M2) representing the undisturbed condition to explore the impact of disturbance on demographic performance and persistency. The use of alternate scenario for modelling the impact of disturbance on the populations is critical as disturbance has often been reported to significantly impact λ. The asymptotic population growth rate (λ) is the dominant eigenvalue of the population matrix and is an important parameter for studying metapopulation dynamics. The change in λ has important implications to the persistency of species[12,13]. M1 matrix contained the vital rate elements that were estimated from the actual number of survivals in the demographic plots, while M2 matrix contained vital rate elements that were estimated by adding actual survivals, including those plants that would have survived if there was no apparent disturbance. During estimation of M2 matrix, care was taken to include those individuals only whose mortality was caused by palpable disturbances. These include: (i) human-induced micro-landslides, (ii) mortality caused by weeding activities in adjoining tourist sites, (iii) apparent deracination and (iv) disappearance of individuals from permanent plots due to miscellaneous activities, including collection of plants for their medicinal use.

Parameterization

A RAMAS Metapop 5.0 application was used to construct a demographic metapopulation model. Stage-wise survival and fecundity were summarized according to Akçakaya[14].

The parameters that were included in the model are vital rates, demographic and environmental stochasticity, and initial population structure/stage abundance. Constraints were imposed within RAMAS Metapop to ensure that all simulated survival rates lie within the bounds of 0.0 and 1.0 with minimal truncation of the distribution. As part of RAMAS algorithm, environmental stochasticity was modelled through introducing random fluctuations in stage-specific fecundities and survivals. For this, the program assigns during each time step to each transition rate, a random value drawn from a specified log–normal distribution whose mean and standard deviation are given by the empirical matrices. A log–normal distribution for stochastic simulations was chosen because several matrix elements had small mean values, but large standard deviations[15,16]. There was no record of catastrophic event in the habitat, as such changes in population size reflected true environmental and demographic stochasticity. Demographic stochasticity was modelled using

Table 1. Number of populations and total number of sampling plots, the data from which were used for metapopulation modeling

Species	Habitat	No. of populations	No. of plots in each population	Total no. of plots	Plot size (m^2)
Paris polyphylla	Continuous forests (CF)	7	5	35	4
	Forest fragments (FF)	4	5	20	4

Table 2. Asymptotic growth rate (λ) of continuous forests (CF) and forest fragments (FF) populations in base model (M1) and alternate model (M2) scenarios

Population	M1	M2	Difference (%)
CF	0.992	0.976	1.6
FF	0.716	0.662	5.4

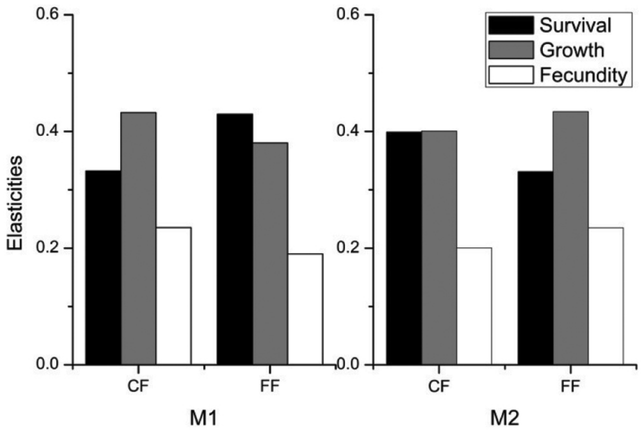

Figure 1. Elasticity values of survival, growth and fecundity in M1 and M2 scenarios.

binomial distribution[17,18]. All simulations were run with 1000 replications and projected to 100 years. Simulation experiments were also conducted to explore the scope for management and recovery of the species.

Results

Deterministic analysis

The asymptotic growth rate (λ) fell below 1.0 in all scenarios depicting a decline in population size with time. In the base scenario (M1), CF populations had a mean $\lambda = 0.976$, while FF had $\lambda = 0.662$. In the alternate scenario (M2), CF populations had a mean $\lambda = 0.992$ and FF had $\lambda = 0.716$ (Table 2).

All three demographic processes, i.e. fecundity (*F*), growth (*G*) and survival (*L*) contributed to λ. Demographic contribution to overall growth of the population by different phases of the life cycle was represented by the relative sensitivity of survival, growth and fecundity to λ. A variation in the elasticity values was seen between CF and FF and also among groups in M1 and M2 (Figure 1). However, like a true iteroparous herb, survival had the highest elasticity value in all populations followed by growth and fecundity. On the other hand, fecundity had the lowest elasticity value in both M1 and M2, signifying that it had least contribution to λ.

Element-wise, the contribution of growth to λ in CF both for M1 and M2 models was highest while in FF the highest contributor in the matrix was the survival of reproductive individuals in M1 and growth in M2 (Table 3). The vital rate elements involving reproductive stage had relatively high elasticity values, which suggested a significant contribution of the stage to λ. To further accentuate and identify the relative importance of each vital rate element to population growth, a proportional change of 10% of each element was made one at a time, while keeping all others constant and noting the ensuing change in λ. This quantitatively identified the effect of change in vital rates on population growth. In Table 3, the actual percentage change in λ resulting from 10% change in the respective elements is given within parenthesis.

Stochastic risk analysis

The trajectory of the abundance of the metapopulation through time was different between M1 and M2 scenarios (Figure 2). The model predicted a stochastic trend with possibility of growth at a few time steps, usually a characteristic feature of a stable population. The overall trend in M1 predicted a gentle decline in metapopulation size with time while M2 typically had an unpredictable trajectory with growth and decline in most time-steps. The trend observed in both the models was a function of their corresponding λ values with M1 having lower λ value and hence the progressive decline in abundance with time.

Probability of extinction

The extinction curve exhibited a wide disparity in isolated scenarios between FF and CF populations, where the former was highly skewed while the latter was relatively smooth (Figure 3). Noticeably, FF was expected to decline early with time in both M1 and M2 scenarios. The risk of extinction of CF populations in isolation and with

Table 3. Elasticity value of each matrix element in M1 and M2 scenarios for CF and FF populations

		CF		FF	
Matrix element/transition	Matrix code	M1	M2	M1	M2
Seedling survival	a_{11}	0.0734 (0.743)	0.0713 (0.728)	0.0932 (0.959)	0.0807 (0.890)
Seedling to adult transition	a_{21}	0.1973 (1.932)	0.1992 (1.934)	0.1902 (1.774)	0.2003 (1.849)
Seedling to reproductive transition	a_{31}	0.0379 (0.380)	0.0356 (0.363)	–	–
Adult survival	a_{22}	0.0598 (0.606)	0.0711 (0.627)	0.0870 (0.894)	0.0753 (0.833)
Adult to reproductive transition	a_{32}	0.1973 (1.917)	0.1992 (1.934)	0.1902 (1.818)	0.2003 (1.902)
Reproductive survival	a_{33}	0.1989 (2.031)	0.1888 (1.998)	0.2493 (2.598)	0.2430 (2.438)
Fecundity	a_{13}	0.2353 (2.283)	0.2348 (2.285)	0.1902 (1.841)	0.2004 (1.918)

Table 4. Threat categorization of *P. polyphylla* according to IUCN criteria (version 3.1)

Extinction risk (%)	Time (years)	Status
5	10	Critically endangered
20	20	Endangered
>10	100	Vulnerable
<10	100	Lower risk
Status of *P. polyphylla* in Sikkim Himalaya		
85	100	Vulnerable

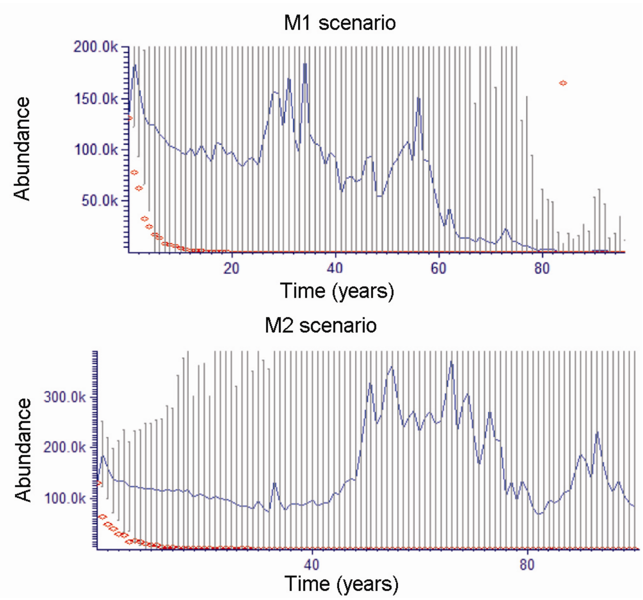

Figure 2. Comparison of expected metapopulation change in M1 and M2 scenarios over 100 years. The mean and 95% confidence intervals of the means after 1000 replications are presented. Minimum and maximum populations are represented by red arrows. Some of the maximum confidence intervals and range are not shown to confine the scale of the curve for better representation.

metapopulation as a whole was almost identical throughout in all projections. The risk of CF in M1 was 0.83, while for the metapopulation scenario it was 0.85. The M2 projected comparatively lower risks with 0.43 extinction risk of CF and 0.42 of the entire metapopulation.

Taking the M1 extinction curve which is the scenario projected from actual survival data as the basis, *P. polyphylla* was estimated to have >10% extinction risk in 100 years and was therefore a vulnerable species in the Sikkim Himalaya (Table 4).

Exploration of management options

Simulation experiments were conducted to estimate the scope for recovery that can be achieved by introducing individuals into the habitat. The primary goal was to explore management intensity required to bring the metapopulation to lower threat status and further to its MVP size state. We chose the contemporary definition of MVP as the minimum metapopulation threshold size at which a species can persist for 100 years with 95% probability. Permutations were done manually and by successively increasing the initial population size (by introduction management) in M1 and M2 model scenarios, a subset of the populations having maximum effect on population growth and persistence was identified. Multiple simulations were run until a desired MVP was reached for each of the three population subsets (Figure 4).

Management exploration using M1 model: The best possible outcome of all the simulation experiments in the M1 model was the introduction of approximately 75,000 reproductive plants three times in 10 years. This is expected to improve the status of the species from vulnerable to lower risk. Further, an introduction of approximately 200,000 individuals for three years in the habitat is required to reach its MVP. However, this is too impractical given that it would require a considerable amount of resources to achieve this target using the M1 model. Realistically therefore, the species is irrecoverable under the actual present status (base scenario). Seedling and adult stages introduction did not give better result.

Management exploration using M2 model: Management scope showed a more promising result with the M2 model. While introduction of seedling and adult stages showed better effect in reducing the risk of decline compared to M1, it did not yield results practical enough for implementation in the real world. On the other hand, introduction of reproductive individuals did produce a viable solution in meeting the management and conservation target. The introduction of 3500 reproductive plants three times in 10 years is expected to bring down the status of the species from vulnerable to lower risk, which is >10% in 100 years (Figure 4). Successive introduction to 9100 individuals is estimated to take the metapopulation to its MVP size.

Thus three MVPs were determined in both M1 and M2 models as designated by red intercepts (Figure 4). The least number of individuals that can be introduced in the model to reach >5% extinction risk in 100 years was taken as the effective MVP size. This was achieved by the introduction of reproductive subsets only in both the models.

Discussion

RAMAS software is widely used for age and stage-based metapopulation modelling; and it is currently the primary application used for coupling climate and demographic models[19,20]. Deterministic analysis highlighted the declining state of *P. polyphylla* metapopulation in which growth rate was estimated to be low in both CF and FF populations. FF populations had lower growth rate than CF populations, which may be attributed to reduced habitat size and quality. In comparison to M1, the M2 model had higher growth rates both in CF and FF, which indicated that disturbance had a negative effect on λ. Similar results were also reported by earlier workers[21].

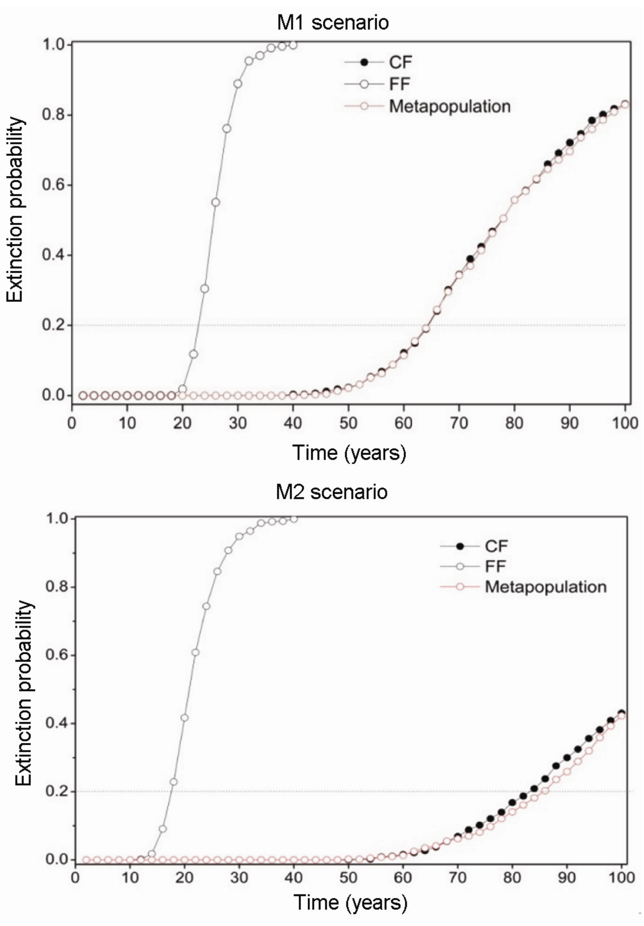

Figure 3. Extinction probability of *P. polyphylla* in M1 and M2 scenarios.

The contribution of different demographic processes to population growth is typical of a perennial plant species, where survival and growth contributed maximum[22]. However, in M2 scenario in CF, the importance of growth and fecundity was reduced in the absence of disturbance (M2), and the role of survival was increased. The opposite was observed in FF where in the absence of disturbance (M2), the role of growth and fecundity was increased and that of survival was decreased. The reason for this may be that certain factors that are intrinsic and population-specific could have contributed to this pattern. Besides, it could be due to the difference in microclimate between CF and FF habitats. Nevertheless, the definitive conclusion from the deterministic analysis is that in the absence of disturbance, the relative role of fecundity in CF was undermined while it increased in FF, and in all cases survival and growth were important for the persistency of the species. This was true perhaps more conspicuously on survival and growth of reproductive stage individuals, as four out of seven matrix elements had comparatively high elasticity values in all population groups and scenarios.

The extinction risk of CF was much lower than FF, which naturally corresponds to their respective growth rate and initial population size being higher in CF. As such, extinction risk is also a function of its growth rate[23] and initial population size as observed by Yates and Ladd[24]. The extinction risk predicted in the actual scenario (M1) differed widely from the alternate scenario (M2), where the former projected 0.85 extinction probability in 100 years and the latter projected 0.42 for *P. polyphylla* metapopulation. The difference of 43% in the risk of decline strongly portrayed the negative role of disturbance and forest fragmentation on the persistence of the metapopulation. Even so, under the predicted risks of both model scenarios, the species is placed under 'vulnerable' status following IUCN criteria. While IUCN has not given any quantitative criteria for 'lower risk', it is suggested that that the same criteria given for MVP, i.e. 5% risk in 100 years may be assigned.

Simulation experiments revealed that the species can be recovered to 'lower risk' with appropriate management intervention. There are two important outcomes from the experiments – first, the huge difference in extinction risk between M1 and M2 is reflected in the conservation exploration where management is seen to be realistic only under M2, i.e. disturbance-free scenario.

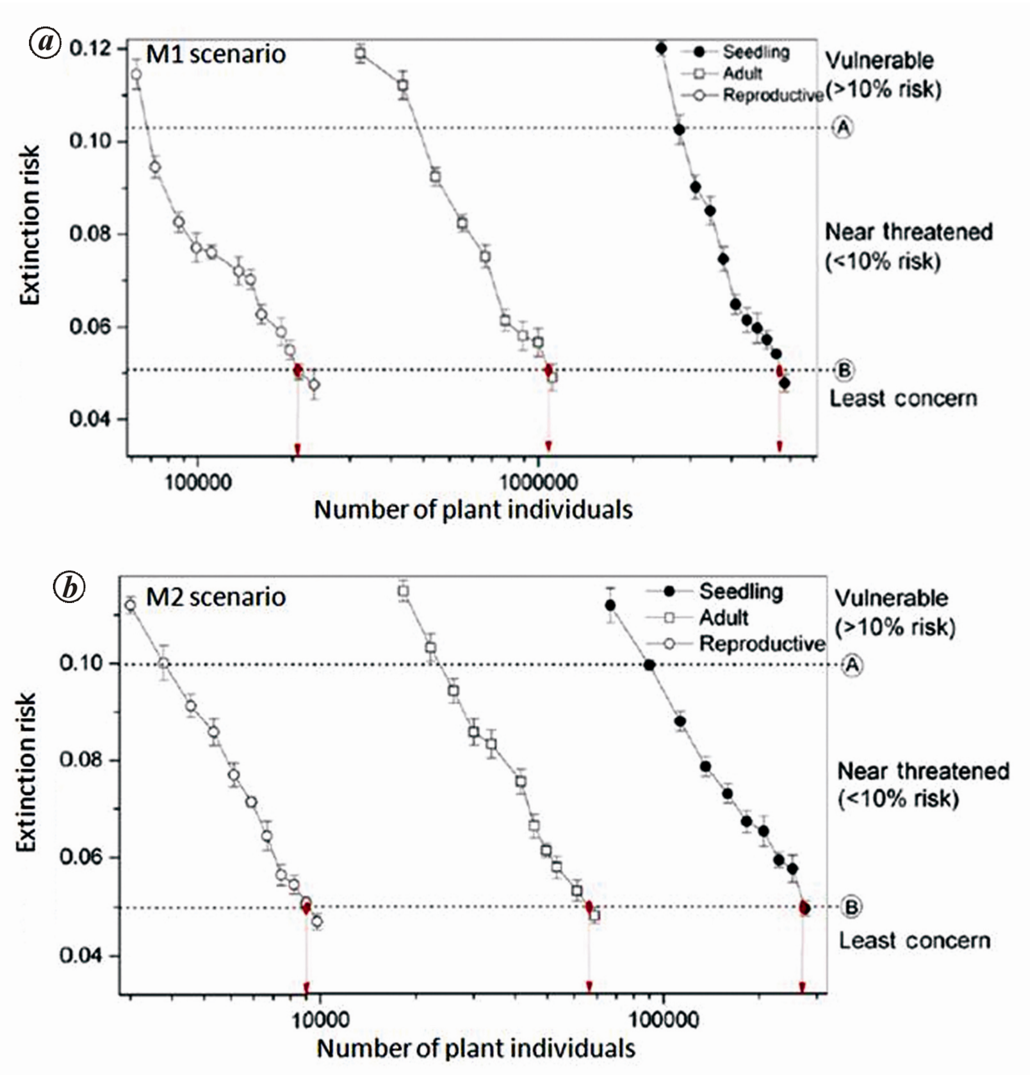

Figure 4. Impact of introduction of seedling, adult and reproductive individuals on extinction risk in (***a***) M1 scenario, (***b***) M2 scenario (Red arrows are drop-down intersection of the three plots at 5% extinction risk, which is the minimum number of individuals required to be introduced to reach minimum viable population size).

Therefore, there is a need to protect the habitat and/or metapopulation and more importantly, the populations in CF. Protection of population will work in tandem with introduction management to strengthen the population size, and it would require the metapopulation to reach its MVP size for its ensured persistency. This is in agreement with Shoemaker *et al.*[25] who proposed that while applying MVP for long-lived species, protection of population can serve as a viable option for conservation.

Secondly, while the introduction of any life-stage can mathematically meet the conservation target, the reproductive one is the only effective one that yielded results practical enough for adoption and implementation. The importance of the reproductive stage as observed in the elasticity values is therefore, accentuated in the experiments for its significance in the conservation of the species.

Conclusion

It is not necessary that the best management option reported and suggested in this work be followed verbatim, as there is likely to be constraint of resources. However, the bottom line is that the metapopulation is expected to perform better with introduction management and also protection of habitat because extinction risk may increase if habitat management is lacking[26]. Continuous monitoring and studies are also essential to adapt and modify long-term management activities.

For a PVA or model to have a precise quantification on cost-effectiveness of management alternatives at different seasons and stages of a metapopulation, more field information needs to be obtained[27]. From the perspective of a developing nation and India in particular, the present study serves as the pioneering attempt at using PVA and

MVP measures for conservation of species. While it is true that conservationists working in developing countries lack the resources to estimate MVPs accurately for conservation targets, this work suggests that it is feasible for species with limited distribution in a given landscape. It would be a fruitful endeavour if the present work could help initiate a more advanced metapopulation model in the country using time-series population and landscape data. This can form the basis for policy making in conservation efforts of priority species.

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