Popul Ecol (2008) 50:227–237
DOI 10.1007/s10144-008-0079-3

ORIGINAL ARTICLE

Conservation prospects for threatened Vietnamese tree species: results from a demographic study

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Received: 17 September 2007 / Accepted: 20 January 2008 / Published online: 8 March 2008

Abstract Given that changes in population size are slow, information on future prospects of long-lived tree species is necessarily obtained from demographic models. We studied six threatened tree species in four Vietnamese protected areas: the broad-leaved *Annamocarya sinensis*, *Manglietia fordiana* and *Parashorea chinensis*, and the coniferous *Calocedrus macrolepis*, *Dacrydium elatum* and *Pinus kwangtungensis*. With data from a 2-year field study on recruitment, growth and survival, we constructed matrix models for each species. All species showed continuous regeneration, as indicated by annual seedling recruitment and inverse J-shaped population structures. To evaluate the future prospects of our study species, we calculated three parameters: (1) asymptotic growth rates (λ) from matrix models indicated significant population declines of 2–3%/year for two species; (2) population trajectories for 50–100 years showed slight population declines (0–3%/year) for five species; and (3) the reproductive period required for an adult tree to replace itself was excessive for three of the six species, suggesting that these species presently have insufficient recruitment. Overall agreement of the three parameters was low, showing that reliance on just one parameter is risky. Combining the three parameters we concluded that prospects are good for *Dacrydium* and *Parashorea*, worrisome for *Annamocarya*, *Manglietia* and *Pinus*, and intermediate for *Calocedrus*. We argue that conservation should involve strict protection of (pre-)adult trees, as their survival is crucial for population maintenance in all species (high elasticity). For species with poor demographic prospects, active intervention is required to improve seedling and tree growth, enrich populations with seedlings from controlled germination, and restore habitat. Finally, our study suggests that these conservation measures apply to long-lived trees in general, given that their demography is highly similar. Such measures should be taken before populations decline below critical levels, as long-lived species will respond slowly to management.

Keywords Conservation strategy · Elasticity analysis · Matrix population models · Population dynamics · Protected areas · Threatened tree species

Introduction

Tropical and subtropical forest areas have declined at an alarming rate over the past decades (Achard et al. 2002), particularly in southeast Asia (Whitmore 1997; Sodhi et al. 2004). As a consequence, many tree species have lost a substantial part of their habitats and have become rare, due either to their restricted distribution or to their low abundance. This phenomenon is illustrated by the large number of critically endangered (477), endangered (333) and vulnerable (962) tree species in southeast Asia

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Electronic supplementary material The online version of this article (doi:10.1007/s10144-008-0079-3) contains supplementary material, which is available to authorized users.

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[World Conservation Union (IUCN) 2006]. The survival of such endangered species is strongly dependent on protected areas (Bawa and Ashton 1991). Even within protected areas, isolated populations of endangered species may be vulnerable to local extinction due to demographic stochasticity or lack of genetic variation (Menges 1992; Lande 1993; Oostermeijer et al. 2003). It is therefore important that the viability of remaining populations of threatened tree species be evaluated to identify what factors determine their fate and what stages in the life-cycle are most important for their survival. To address these issues, studies on spatial distributions, densities, genetic variation, or cultivation of the species are not sufficient, as they do not provide information on likely population changes in time (Schemske et al. 1994; Dowe et al. 1997; Keith 2000). Demographic studies, in contrast, do provide such information and have been shown to be useful in evaluating the viability of threatened populations. Given that population changes in tree species are slow, such studies are necessarily carried out using population models (e.g., matrix models; Harvey 1985; Lande 1988; Silvertown et al. 1996; Menges 2000).

In this paper we present a study on the demography of threatened tree species in Vietnam, a country where natural forest cover declined from 43% in 1943 to 30% in 2003 (Hung 2004). We studied six threatened tree species in four protected areas. All species are on Vietnam's Red List: four are endemic to Vietnam and southern China, and two others are relict species that occur in only a fraction of their historical geographical range [Ministry of Science, Technology and Environment (MSTE) 1996; Nghia 2000]. To our knowledge, ours is the first study that evaluates conservation prospects of southeast Asian tree species using demographic analyses.

We addressed the following questions: (1) Are populations of our study species regenerating naturally? To answer this question, we carried out a 2-year demographic field study in which we examined recruitment and evaluated population structures. (2) What is the future prospect for these species? To this end, we constructed population transition matrices for all six species and calculated population growth rates, survival curves, and ages. (3) What are the most important processes or stages in the life cycle of the species that should be the focus for conservation measures? This question was addressed by our calculating elasticity values from matrix models (de Kroon et al. 2000) and comparing these among vital rates (survival, growth and fecundity) and species. Our study delivered essential information for effective conservation of our study species, and also for threatened tree species in general.

Methods

Study species

We selected six study species using the following criteria: conservation status (i.e., included in Vietnam's Red List), preferably endemic to the region (i.e., preferred as these are strongly understudied species), taxonomically well described (to avoid misidentification), known locations of populations in conservation areas (Nghia 2000), sufficiently large populations for population modeling (i.e., >100 individuals), and from a variety of forest types (i.e., altitudes and locations). A brief description of the six study species (Table 1, referred to by genus name hereafter) is included below, based on MSTE (1996), Nghia (2000) and Hiep et al. (2004). (1) *Annamocarya sinensis*, an endemic species of Vietnam and southern China, is a large deciduous forest tree species. *Annamocarya* occurs in evergreen tropical forests at elevations of 100–600 m. In Vietnam, *Annamocarya* is restricted to several protected areas, but with limited distribution. *Annamocarya* fruits annually, producing heavy (50–60 g) seeds (Thu and Can 1999). (2) *Calocedrus macrolepis* is a conifer that dominates the canopy of subtropical forests in high mountains. Despite its wide distribution (southwest China, Myanmar, Thailand, Laos and Vietnam), this species has become rare due to habitat loss and is represented by only small populations (Wang et al. 2004). In Vietnam, it occurs in small populations in the Central Highland and Ba Vi Mountains in the North. (3) *Dacrydium elatum* is also a coniferous species, occurring in tropical and subtropical rain forests (500–1,800 m) in southeast Asia and Hainan Island (China). In Vietnam, the distribution of *Dacrydium* has severely declined, due to habitat loss, and is currently sparse in central Vietnam. Regeneration of the species has been observed in open and moist forests close to parent trees (Keo 2003). (4) *Manglietia fordiana* is an endemic species of Vietnam and southern China. In Vietnam, *Manglietia* is sparsely distributed in tropical rain forests at elevations from 100 m to 1,000 m. Seedlings are shade-tolerant, and adults reach the forest canopy. Currently, the species is restricted to small populations in protected areas, and it is an important focal species for conservation. (5) *Parashorea chinensis* is a large tree species that reaches the canopy of dense evergreen tropical forests. Both habitat extent and local abundance of *Parashorea* have severely declined strongly due to deforestation and overexploitation. Adult trees of the species are mostly restricted to protected areas. Seeds of the species are small, winged, and wind-dispersed. Abundant natural regeneration is found along streams and in wet open areas. (6) *Pinus kwangtungensis* is a big subtropical coniferous forest tree that is endemic to Vietnam

Table 1 Characteristics of the study species and their status in the IUCN Red List

Species (family)	Maximum height (m)[a]	Maximum DBH (cm)[a]	Main uses	Main threats	IUCN Red List category
Annamocarya sinensis (Dode) Leroy (Juglandaceae)	35	150	Timber Seeds eaten	Habitat loss and fragmentation Overexploitation Low natural regeneration	CR D
Calocedrus macrolepis Kurz (Cupressaceae)	15–25	>100	Timber Incense extracted from wood Young trees used for ornamental purposes	Habitat loss and fragmentation Overexploitation Restricted distribution	EN D
Dacrydium elatum (Roxb) Wall ex Hook (Podocarpaceae)	20–25	50–70	Timber Incense, chemicals for pesticide	Habitat loss and fragmentation Overexploitation Restricted distribution	VU cd
Manglietia fordiana (Hemsl.) Oliv. (Magnoliaceae)	15–20	50–60	Timber	Habitat loss and fragmentation Overexploitation Restricted distribution	EN D
Parashorea chinensis Wang Hsie (Dipterocarpaceae)	70	>100	Timber	Habitat loss and fragmentation High demand for wood Overexploitation	VU cd
Pinus kwangtungensis Chun ex Tsiang (Pinaceae)	15–20	50–70	Timber Resin extraction	Habitat loss and fragmentation Overexploitation Restricted distribution Low natural regeneration	EN D

CR critically endangered, *EN* endangered, *VU* vulnerable, *D* data deficient, *cd* conservation dependent, *DBH* diameter at breast height

[a] Sources: Thu and Can (1999), Nghia (2000)

and southern China. In Vietnam, its distribution is restricted to limestone mountains at 1,200–1,400 m. Is has been reported that only fewer than 100 adult trees of the species remain in the country, and seedlings are rarely found.

Study sites

Our study was performed in four protected areas. Cuc Phuong National Park (21° N–105° E, 2,160 mm rain annually) spans two parallel limestone mountain changes at about 300–400 m altitude. Study plots for *Annamocarya* and *Parashorea* were located in highly diverse forests (canopy height of 25–30 m) in the central valley of the park on flat terrain [250–300 m above sea level (a.s.l.)]. Ba Vi National Park (21° N–105° E, 2,590 mm rain) includes three peaks (>1,000 m a.s.l.), surrounded by plains. The study plots for *Calocedrus* were located at 1,200 m on the peaks, in rather open subtropical evergreen coniferous-broad-leaved forest (canopy 15–20 m), with abundance of bamboos. Plots for *Manglietia* were at lower elevation (900 m) in denser tropical evergreen broad-leaved forest (canopy at 20–25 m). Bach Ma National Park in Central Vietnam (16° N–107° E, 3,600 mm rain) includes forests at different elevations (100–1,200 m). The study plots for *Dacrydium* were at 1,000–1,200 m in evergreen subtropical forest with a canopy of 15–20 m height. Hang Kia–Pa Co Nature Reserve (20° N–104° E, 1,925 mm rainfall) is on the high limestone mountains of Hoa Binh Province and experiences a subtropical climate. The study plots were covered by subtropical coniferous broad-leaved forests (canopy height 15–20 m), in which *Pinus* is one of the dominant canopy tree species.

Data collection

Permanent plots of 2.5–3 ha were established in 2003: three plots for *Annamocarya* ($n = 208$ individuals in total), two plots for *Calocedrus* ($n = 388$), three plots for *Dacrydium* ($n = 432$), two plots for *Manglietia* ($n = 386$), three plots for *Parashorea* ($n = 275$), and three plots for *Pinus* ($n = 263$). At first measurement, all juvenile and adult trees [diameter at breast height (DBH) >5 cm) of the study species in the plots were located, tagged and measured. Measurements were carried out again in 2004 and 2005. On each occasion, DBH and total height were measured, and survival and reproductive status were recorded.

Within the plots, we established random subplots (20 × 20 m) to study seedlings and saplings (<5 cm

DBH). Per species a total 20–60 subplots were established, depending on seedling density, so that we should get at least 100 seedlings for each species. At first measurement in 2003, all seedlings and saplings of the study species in the subplots were searched for, tagged and measured. Parameters measured were total height and diameter at ground level (or DBH if possible). Measurements were conducted again, annually, in 2004 and 2005. Mortality and recruitment of seedlings and saplings were recorded on each occasion.

Data analysis

As the data for the demographic parameters were collected at different plots and in different years, we tested survival and growth rates for differences between plots and years, using analysis of variance (ANOVA), linear, non-linear, or logistic regression models. In the case of no significant difference, data were pooled for the construction of transition matrices.

We related height increase of seedlings (g) and seedling height using linear regression, and we used logistic regressions to relate seedling survival (σ) probability to height.

Tree diameter growth is typically non-linearly related to the initial diameter, with high growth rates for intermediate-sized trees. Therefore, diameter growth was related to DBH, using the Hossfeld IV equation (Zeide 1993):

$$g = \frac{b \times c \times \mathrm{DBH}^{(c-1)}}{\left[b + \left(\mathrm{DBH}^{c/a}\right)\right]^2} \tag{1}$$

where g is DBH growth rate (centimeters per year), and a, b and c are fitted parameters. We used non-linear regression analysis with a least-square loss function to fit this function through observed data on g and DBH.

The relation between reproductive status and DBH was analyzed by logistic regression in order to calculate the probability of reproduction for each category ($Prob\{\mathrm{f}\}_i$).

Construction and analysis of transition matrix

We used Lefkovitch matrix models (Caswell 2001) to project population dynamics. These models use the equation: $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are population structures at time t and $t+1$, and $\mathbf{A}$ is a square matrix containing transition probabilities among categories during a one time step (1 year). When the multiplication of $\mathbf{A}$ and $\mathbf{n}(t)$ is repeated many times, the relative structure and growth rate of the population becomes stable. When a stable size distribution is reached, the dominant eigenvalue (λ) and the right eigenvector of the matrix $\mathbf{A}$ are equal to the growth rate and the stable stage distribution of the population, respectively.

Populations were divided into 14–18 size categories, depending on the abundance and size structure of each population (see Table A1 in Electronic supplementary material (ESM)). For all species, the four smallest categories were based on seedling height: 0–30 cm height, 30–60 cm, 60–100 or 60–120 cm, and from 100 or 120 to reaching 1 cm DBH. The remaining categories were based on DBH: 1–5 cm, 5–10 cm, and continuing with 5-cm wide DBH categories. For the large *Parashorea* different categories were established: from 10 cm to 70 cm DBH in 10-cm wide categories, then in 20-cm wide categories.

Elements (a_{ij}) of matrix $\mathbf{A}$ can be grouped into growth, stasis, or fecundity. Growth elements (G, elements in the sub-diagonal of the matrix) that represent the probability of an individual to grow from one category to the next, were calculated as $G_i = \sigma_i \times \lambda_i$, where λ_i is the probability that a surviving individual in category i moves to $i+1$, σ_i is the survival probability in category i. The value of λ_i was calculated as g_i/c_i, in which g_i is the growth rate in height or DBH for category i (in centimeters per year, at its midpoint) and c_i the category width (in centimeters height or DBH). Stasis elements (P, in the diagonal of the matrix) represent the probability that an individual survives and stays at the same category, and were calculated as $P_i = \sigma_i - G_i$. Fecundity elements (F, the upper row, except for the top-left element) represent the number of seedlings produced by an adult individual. We assumed that all reproductive individuals had the same reproductive output (number of seedlings). Therefore, F was calculated as $F_i = \sigma_i \times Prob\{f\}_i \times f_i$, where $Prob\{f\}_i$ is probability of being reproductive for individuals in category i, and f_i was calculated as the quotient of abundance of new seedlings (per hectare, per year) and abundance of reproductive trees (per hectare).

We estimated the similarity between the stable stage structures resulting from the matrix models and the observed population structures using the similarity index PS (Horvitz and Schimske 1995). $\mathrm{PS} = \sum \min[\mathrm{ops}_i, \mathrm{ssd}_i] \times 100$, where ops_i is the vector of observed population structures, and ssd_i is the vector of stable size distribution. Both vectors were scaled to sum to 1. High values of PS indicate high values of similarity.

Dominant eigenvalues (λ) were calculated (Caswell 2001): if $\lambda > 1$, populations are project to grow, whilst they decrease for $\lambda < 1$. To examine whether λ was significantly different from unity, we calculated the 95% confidence limits of λ with the series approximation approach (Caswell 2001) and using sensitivity and variance of vital rates (survival, growth and reproduction), respectively. As we lacked information on variation in reproductive output among individuals, this was not taken into account in the calculation, thus probably leading to a slight underestimation of the confidence interval. Transient dynamics of the populations were analyzed by multiplication of the population structure by the transition matrices for 50 years and 100 years for all six species. Based on population changes over these periods, we calculated the annual growth rate and compared these values to the value of λ.

The elasticity of vital rates (survival, growth and reproduction), the proportional change in λ due to a proportional change in a vital rate (de Kroon et al. 2000), indicates the importance of vital rates to λ. We calculated the elasticity of vital rates using the approach of Caswell (2001) and Zuidema and Franco (2001). It should be noted that vital rate elasticities differ from those for matrix elements in that they may be negative (if an increase in a certain vital rate leads to a reduction in λ) and that they do not sum to 1 (Caswell 2001).

Lastly, using the transition matrices, we constructed survival curves for each of the six study species following the approach of Cochran and Ellner (1992). We also calculated the age at which reproductive size is reached by calculating the conditional age (τ in Cochran and Ellner 1992) of entering the first reproductive size category.

Results

Size distribution and natural regeneration

The six study species differed considerably in maximum DBH. The largest trees of *Dacrydium*, *Manglietia*, and *Pinus* were just over 60 cm DBH, those of *Calocedrus* 85 cm DBH, while those of *Annamocarya* and *Parashorea* reached more than 100 cm DBH. The variation in maximum size corresponded to differences in forest structure: *Annamocarya* and *Parashorea* occur in forests at low elevation with high canopy height (25–30 m), while the other study species are typically found in forests with lower canopy at higher elevations.

Population structures of the six study species all showed inverse J-shaped curves (Fig. 1), with most individuals present in the seedling and juvenile categories. Although the abundance differed strongly among species, all population structures showed a continuous abundance of individuals without any clear “bottleneck” (Fig. 1). This result suggests that there is continuous regeneration for all study species.

Natural regeneration was observed of all study species in both observation years. For *Annamocarya*, *Calocedrus*, *Dacrydium*, *Manglietia*, *Parashorea* and *Pinus* we counted 5.2, 85, 47, 14.5, 16.3 and 7.3 new seedlings per hectare and per year, respectively (averaged over the 2 years). When expressed per reproductive tree, the number of seedlings produced by a reproductive tree ranged from 1 to 5 among species, without varying much between observation years (Fig. 2).

Vital rates

Survival probabilities of all study species increased from 65–85% for small seedlings (category 1) to 96–99% for adult trees. Survival was positively related to seedling height for all species but *Annamocarya* (see Table A2 in ESM).

Survival percentage of juvenile and adult trees was high (90–99%). The number of dead trees (>1 cm DBH) observed over 2 years was 8, 20, 10, 16, 5 and 5 for *Annamocarya, Calocedrus, Dacrydium, Manglietia, Parashorea* and *Pinus*, respectively. Survival was not significantly related to DBH for trees (logistic regressions, $P > 0.05$), and was therefore calculated as average over various categories (see Table A1 in ESM).

The six study species differed in rate of seedling height increase, with *Manglietia* seedlings growing fastest (>11 cm/year for large seedlings) and *Dacrydium* seedlings growing slowest (<6 cm/year). Seedling height increase was rather variable within size categories, with coefficients of variation of 0.4–0.5. Linear relationships between seedling growth and initial height were established for all species (see Table A3 in ESM).

DBH growth rate for all species increased from low values (0.1–0.2 cm year^{-1}) for small trees to high values (0.4–0.7 cm^{-1}) for mid-sized trees (20–50 cm DBH), and then gradually decreased to lower values again. DBH growth patterns could be well described using Hossfeld curves (Eq. 1), with R^2 values of 0.6–0.75 (see Table A4 in ESM).

Reproductive status was strongly related to tree size in all species (see Table A5 in ESM). In general, reproduction started at 10–20 cm DBH, with somewhat lower values for conifers than for broad-leaved species. The size at which 90% of the individuals were reproductive, ranged from 30 cm to 70 cm DBH among species.

Matrix model output

As no significant differences in vital rates were found between study years or among plots (statistical results not shown), one transition matrix was constructed for each species (Table 2).

The values for the similarity index PS were high (range 85 for *Annamocarya* and *Pinus* to 95 for *Calocedrus*), indicating that our models provided realistic projection of the observed population structures. The asymptotic population growth rates (λ) of the six study species were all slightly below 1 (Fig. 3), which suggests that populations are slowly declining. Nevertheless, the 95% confidence

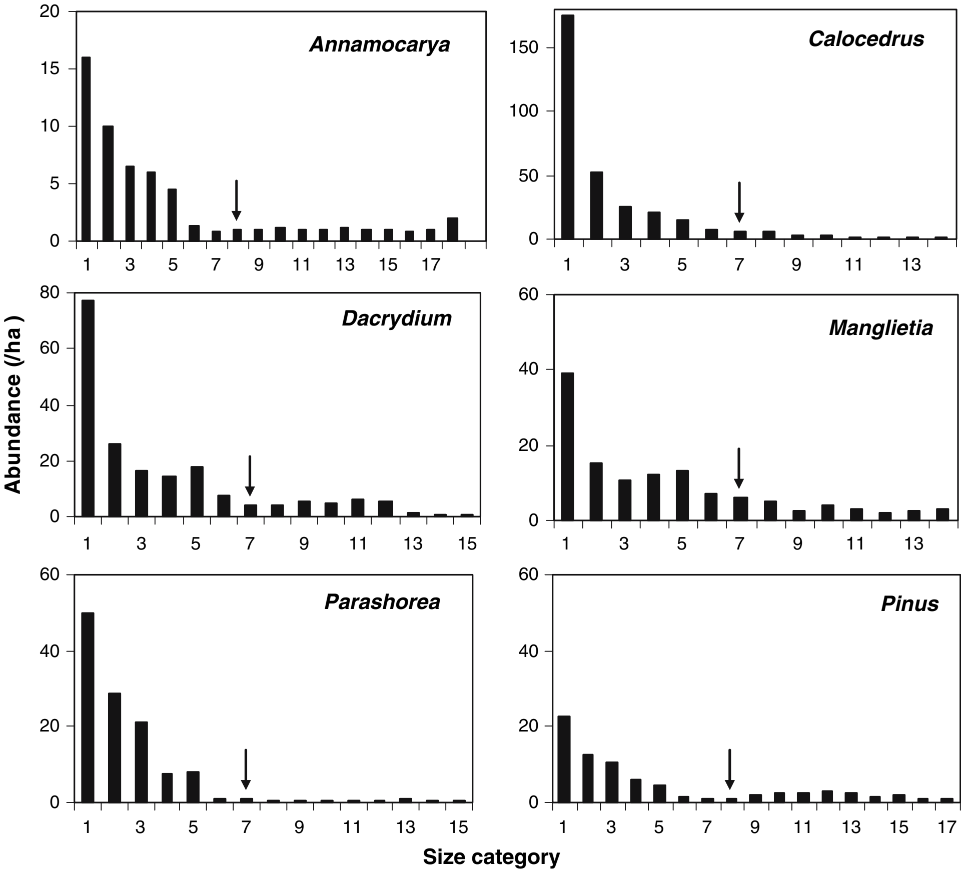

Fig. 1 Population structures of six threatened Vietnamese tree species in four protected areas. The first four size categories are for seedlings (<1 cm DBH), the rest for trees (see "Methods"). *Arrows* show the category in which trees start reproducing

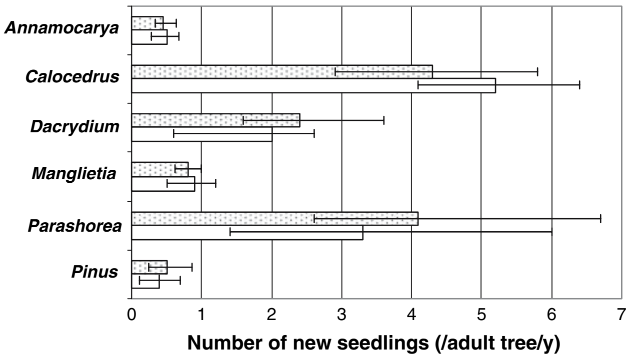

Fig. 2 Recruitment of six threatened tree species in Vietnam, expressed as number of new seedlings appearing per year and per adult tree. *Dotted bars* are for 2003–2004, *open bars* for 2004–2005. *Error bars* indicate the maximum and minimum values for the study plots

intervals of λ included the value 1 for four out of six species (*Dacrydium*, *Manglietia*, *Parashorea* and *Pinus*). For these species, there is no indication of a significant decline in size of the studied populations. For the two other species—*Annamocarya* and *Calocedrus*—the 95% confidence limits did not include 1, suggesting that these populations are declining.

As λ is the asymptotic population growth rate when the population structure is equal to stable stage structure, its value may differ from the population growth rate obtained when projecting the present population structure for a limited period of time (based on the transient dynamics of the population). For the comparison, we therefore calculated the annual population growth rate based on the matrix projection of 50 years and 100 years. For all six species, the projected population growth rates based on transient dynamics were close to asymptotic growth rates (λ; Fig. 3). The projected growth rates based on 50-year projections were lower than unity for five of the six species, while for those based on 100-year projections this was the case for all species.

The estimated age at first reproduction varied among species, from 35 years for the relatively fast-growing *Manglietia* to 60 years for the slow-growing *Pinus*. We obtained these age values with survival curves to estimate the average fraction of newborns that becomes reproductive. The results (Fig. 4) show that only a very small fraction (0.1–1.0%) of the seedlings recruited in the population survives to reproductive size. This value varied strongly among species, being one order of magnitude larger for *Dacrydium* and *Parashorea* than for *Manglietia*.

Table 2 Annual transition matrices for the study species. Columns are stages at time *t*, rows at time *t* + 1

Annamocarya

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	0.744	0	0	0	0	0	0	0.12	0.15	0.18	0.22	0.26	0.32	0.38	0.42	0.44	0.45	0.44
2	0.109	0.729	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.131	0.750	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0.118	0.800	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0.080	0.875	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0.019	0.896	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0.039	0.917	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0.065	0.897	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0.085	0.882	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0.100	0.872	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0.110	0.867	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0.115	0.865	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0.116	0.925	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0.056	0.931	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.051	0.938	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.044	0.944	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.037	0.950	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.031	0.950

Calocedrus

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.683	0	0	0	0	0	1.38	2.70	3.78	4.30	4.53	4.53	4.51	4.51
2	0.091	0.691	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.110	0.768	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0.070	0.808	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0.0742	0.898	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0.015	0.930	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0.028	0.917	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0.042	0.906	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0.052	0.898	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0.060	0.8929	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0.0654	0.924	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0.034	0.925	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0.033	0.923	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0.030	0.953

Dacrydium

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0.699	0	0	0	0	0	0.28	0.58	0.99	1.36	1.60	1.72	1.78	1.80	1.77
2	0.085	0.727	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.104	0.780	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0.095	0.842	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0.079	0.930	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0.029	0.924	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0.0429	0.928	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0.059	0.918	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0.070	0.9107	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0.0764	0.907	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0.080	0.905	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0.082	0.9057	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0.0814	0.9074	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0.080	0.916	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.071	0.970

Manglietia

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.609	0	0	0	0	0	0.16	0.27	0.42	0.56	0.67	0.74	0.77	0.76
2	0.135	0.598	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.184	0.653	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0.187	0.726	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0.014	0.896	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0.014	0.913	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0.037	0.916	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0.067	0.891	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0.092	0.874	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0.110	0.865	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0.119	0.863	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0.121	0.867	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0.116	0.879	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0.101	0.940

Parashorea

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0.700	0	0	0	0	0	0.78	1.17	1.64	2.13	2.58	2.94	3.28	3.50	3.57
2	0.101	0.704	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.136	0.793	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0.096	0.819	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0.118	0.901	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0.019	0.922	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0.039	0.946	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0.037	0.930	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0.0527	0.9238	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0.0594	0.924	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0.059	0.929	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0.055	0.935	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0.048	0.964	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0.019	0.970	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.014	0.983

Pinus

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	0.540	0	0	0	0	0	0	0.21	0.28	0.33	0.37	0.39	0.40	0.41	0.41	0.41	0.40
2	0.106	0.636	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.171	0.787	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0.123	0.801	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0.119	0.911	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0.009	0.935	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0.025	0.935	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0.045	0.925	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0.062	0.915	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0.073	0.910	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0.077	0.911	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0.076	0.916	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0.071	0.9227	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0.0647	0.930	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0574	0.937	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.050	0.937	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.043	0.960

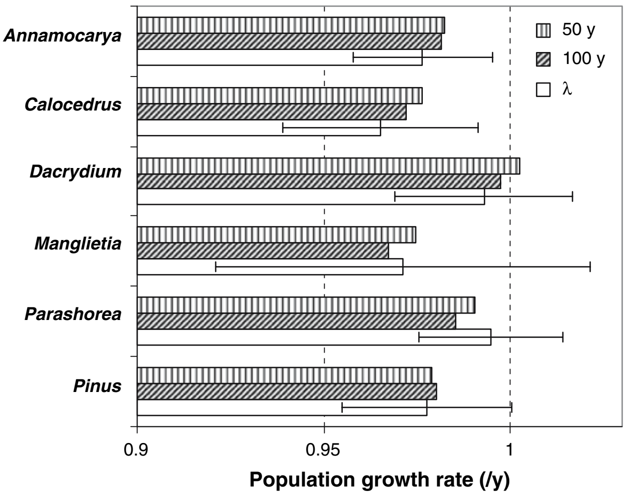

Fig. 3 Three estimates of population growth rates for six threatened Vietnamese tree species obtained from matrix models. Shown are the projected population growth rates based on transient dynamics over 50 years and 100 years, as well as the asymptotic population growth rate (λ, with 95% confidence interval)

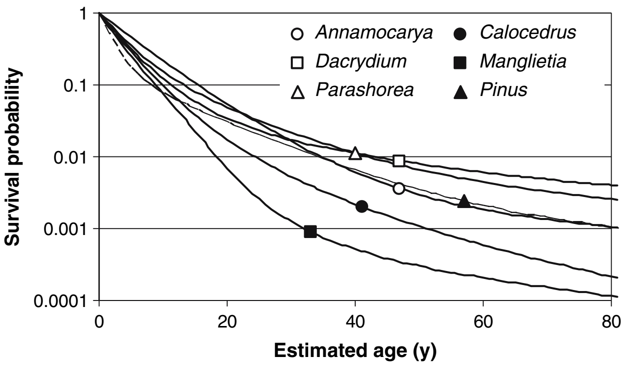

Fig. 4 Survivorship curves for six threatened tree species in Vietnam based on matrix models. *Symbols* indicate the age at which trees start reproducing (conditional age τ, Cochran and Ellner 1992) and the corresponding survival probability to that age. Note that the *Y* axis has a logarithmic scale

Elasticity analysis showed that, in all species, survival was the most important vital rate for population growth, followed by growth and fecundity (Fig. 5). In particular, survival of juvenile and small reproductive trees (categories 5–8) was most important for population growth.

To compare elasticities of vital rates between our study species and other tree species for which matrix models are available, we constructed a triangle ordination using elasticities of vital rates, following Franco and Silvertown (2004; Fig. 6). We found that the elasticity distribution over vital rates of our study species was consistent with that for other tree species, represented by points close to the survival vertex of the triangle, indicating strong importance of survival for population maintenance.

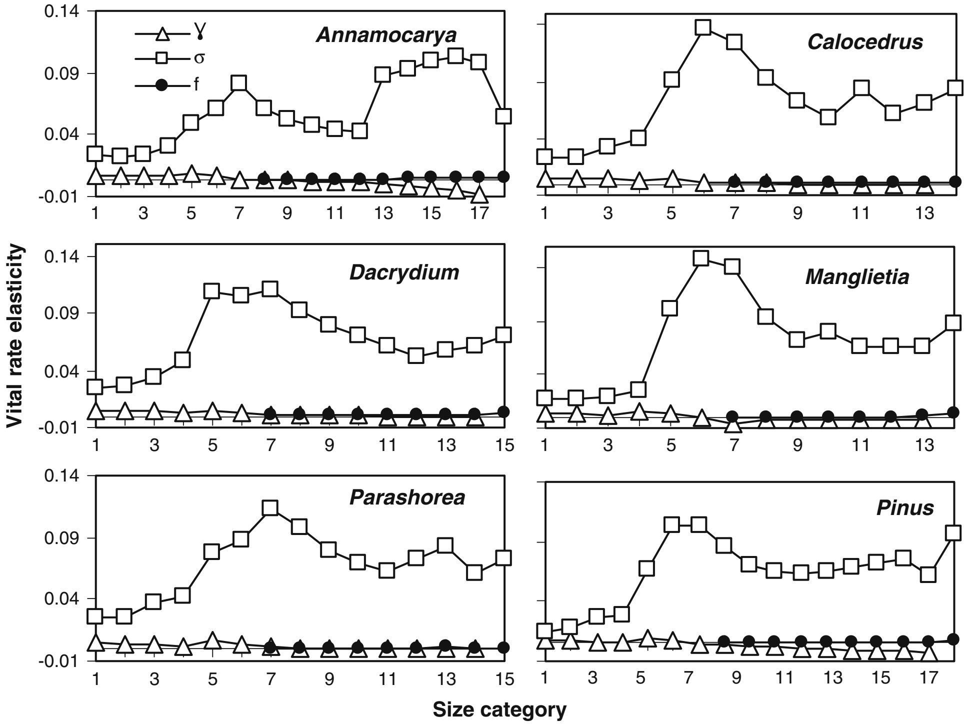

Fig. 5 Vital rate elasticity for six threatened Vietnamese tree species. Shown are elasticities for growth (γ), survival (σ) and fecundity (*f*), denoting the proportional change in λ due to a proportional change in that vital rate. The first four size categories are for seedlings (<1 cm DBH), the rest for trees (see "Methods")

Discussion

Differences between species

Although our study species are all long-lived trees species that reach the forest canopy as adults, they show differences in performance that are probably caused by variation in habitat among species. For instance, DBH growth rates of *Calocedrus*, *Dacrydium*, and *Pinus* were relatively slow (see Table A1 in ESM), probably in response to low temperatures and shallow soils, typical for mountain habitats. On the other hand, these species showed relatively high juvenile growth rates, which may be attributed to the typically open structure of montane forests.

In spite of the clear differences in habitat, ecology, and tree performance, the population dynamics of our study species were highly comparable, as indicated by similar elasticities (Figs. 5, 6). The distribution of elasticity values of our study species is typical for that of long-lived tree species, with high importance of survival for population growth, and low importance of reproduction (Franco and Silvertown 2004).

Natural regeneration

Ultimately, population maintenance depends on natural regeneration. We found that all six species were regenerating naturally in all sites and in both observation years.

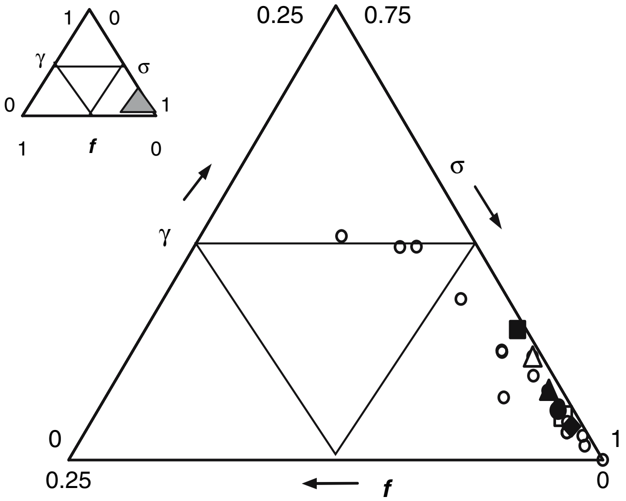

Fig. 6 Position of six threatened Vietnamese tree species in relation to that of 22 reference tree species [*open circles*, from Franco and Silvertown (2004)] in a triangular ordination of vital rate elasticity values (survival, σ; growth, γ; fecundity, *f*). The six study species are indicated by *open triangle* (*Annamocarya*), *open square* (*Calocedrus*), *open diamond* (*Dacrydium*), *filled triangle* (*Manglietia*), *filled circle* (*Parashorea*) and *filled square* (*Pinus*). Absolute values of elasticity were used, these were summed over categories per vital rate and scaled to sum to 1

Our results are consistent with those of previous studies on recruitment for some of the study species (Thu and Can 1999; Nghia 2000; Keo 2003). Another indication of natural regeneration was observed in population structures: all species showed continuous and inverse J-shaped size distributions, without signs of regeneration bottlenecks (e.g., Peres et al. 2003). However, we emphasize that unfavorable recruitment conditions outside protected areas due to anthropogenic disturbances may lead to population structures that differ from the ones we observed inside parks.

Inverse J-shaped size distributions are typically found for forest tree species with good recruitment (Poorter et al. 1996; Zuidema and Boot 2002). Nevertheless, it is important to note that as such, an inverse J-shaped population structure and/or continuous recruitment does not indicate that recruitment is *sufficient* to maintain populations. Populations that suffer from insufficient recruitment may still present continuous recruitment and an inverse J-shaped distribution.

Future prospects of populations

To determine whether natural regeneration is sufficient for population maintenance we calculated three measures. First, asymptotic growth rates (λ) proved to be significantly below 1.0 for two species, suggesting that, in the long run, their populations will decline. This result needs to be interpreted with caution, as we estimated confidence intervals without taking into account variation in reproduction. Second, transient population growth rates over the next 50–100 years (Fox and Gurevitch 2000; Van Mantgem and Stephenson 2005) suggested annual declines of 1–3% in population size for five of the six species (Fig. 3). Transient population growth rates were similar to asymptotic rates (λ), but they should be interpreted cautiously, bearing in mind the uncertainty in their values, which is probably comparable to that in λ.

The third measure of future population growth that we applied is seldom used but seems suitable for evaluating population prospects. It combines information on recruitment and ages to check whether an adult tree produces sufficient seedlings to replace itself. For example, in *Manglietia*, survival to adult size amounts to 0.1% (Fig. 4), implying that an adult tree should produce 1,000 seedlings in its entire reproductive life to replace itself. At the rate of fewer than one seedling per year that we observed (Fig. 2), this would take over 1,000 years. In a similar way, we calculated the required reproductive life span for the other species: this was 480 years for *Annamocarya*, 70 years for *Calocedrus*, 52 years for *Dacrydium*, 25 years for *Parashorea* and 580 years for *Pinus*. For *Annamocarya*, *Manglietia* and *Pinus*, reproductive periods are far longer than maximum ages estimated from matrix models and ring counts (ranging from 150 years to 250 years, Chien 2006). These calculations are based on the recruitment rates estimated over the 2-year study period and assume that there are no strong temporal fluctuations in recruitment rate. Nevertheless, to our knowledge, all study species fruited annually and just one (*Annamocarya*) has been reported to exhibit inter-annual variation in fruiting (Nghia 2000, peak fruiting every 3–4 years, P. D. Chien, personal observation).

We combined the results obtained from the three measures (Table 3) to draw conclusions on future prospects for populations of our study species. It appeared that there was little congruency among the three measures. The discrepancy between asymptotic and transient population growth rates can be explained by the lack of confidence intervals for the latter, which therefore tends to provide a more pessimistic picture. The results from the offspring calculations and growth rates may differ, as they are calculated in very different ways: survival curves and recruitment rates in the offspring calculations use only the survival rates from the transition matrix (Cochran and Ellner 1992) and the observed number of recruits, while growth rate calculations use the entire transition matrix. Clearly, these differences underscore the limitation of using just one parameter to assess future prospects of threatened species, as is often done (Floyd and Ranker 1998; Bierzychudek 1999).

Combining our findings, we concluded that the future prospects for *Dacrydium* and *Parashorea* are good, as their populations are not declining and recruitment is sufficient to replace adult trees. In contrast, the future prospects for *Annamocarya*, *Manglietia* and *Pinus* are worrisome: although there is no evidence for population decline based on the asymptotic population growth rates for two of these species, the number of recruits produced per year is clearly insufficient to guarantee replacement of the adult tree for all three species. For *Calocedrus*, populations are projected

Table 3 Comparing three measures of future prospects for populations of six threatened Vietnamese tree species

Species	Future prospects of populations based on		
	Asymptotic growth rate (λ)[a]	Transient growth rate[b]	Reproductive output[c]
Annamocarya	−	−	−
Calocedrus	−	−	+
Dacrydium	+	+	+
Manglietia	+	−	−
Parashorea	+	−	+
Pinus	+	−	−

[a] + Indicates $\lambda \geq 1$; − indicates $\lambda < 1$

[b] + Indicates projected increase over 50–100 years; − indicates projected decline

[c] + Indicates sufficient offspring to replace adult tree; − indicates insufficient offspring

to decline, but recruitment appears to be sufficient for adult replacement.

Our study was not intended to provide explanations for the projected population decline or the insufficient recruitment. Nevertheless, some potential causes for these results can be provided. These include genetic impoverishment in small populations (Lande 1988; Yao et al. 2007), demographic and environmental stochasticity (Menges 1992, 2000; Lande 1993), and the slow and gradual population decline that may be inherent to relict species (Pico and Riba 2002). Clearly, further studies on genetic diversity, stochastic effects and long-term population changes are required if we are to understand population development better.

Finally, all three measures presented here were based on a short-term demographic study and do therefore not take into account sporadic events leading to peaks in recruitment or mortality. To the extent that such events drive the long-term population dynamics of our study species, the conclusions on population prospects presented here need to be refined.

Implications for conservation

Our results suggest that successful protection of the six study species requires various conservation measures. First, elasticity analysis showed that juvenile and adult trees are most important for population maintenance (cf. Zuidema and Boot 2002; Franco and Silvertown 2004; Kwit et al. 2004). Strict protection of individuals in these stages is therefore crucial to population maintenance. Second, for species with insufficient recruitment (*Annamocarya*, *Manglietia* and *Pinus*) and declining populations, it will be necessary to conduct additional measures to reverse projected population declines. Although our study did not evaluate such conservation measures, the large variation observed in growth rates of seedlings suggests that there would be scope for liberation thinning to increase average growth rates (cf. Batista et al. 1998; Kwit et al. 2004). The conservation measures mentioned here are most likely also applicable to other tree species with similar problems of population decline and insufficient regeneration, as there is strong congruence in population regulation of long-lived tree species (Fig. 6; Kwit et al. 2004).

Finally, the dynamics of long-lived species has the advantage that declines take place at a slow pace, thus providing more time for conservation measures to be taken. Nevertheless, slow dynamics also implies that it will take a long time for such measures to result in population increases. Therefore, taking action before populations have declined below critical levels is of utmost importance, and this should be accompanied by close monitoring of population size and recruitment.

Acknowledgments We are very grateful to Le Van Binh, Vu Van Can, Tran Quang Chuc, Le Phuong Trieu, Bui Van Duong, Duong Ngoc Anh, Luu Cu, Nguyen Van The, Dinh Duc Huu, Le Van Thu, Pham Quang Vinh and others for their assistance with the field work and for discussions. We thank the managers of the four protected areas for granting permission and providing assistance. We acknowledge Marinus Werger, Francis Putz, Takashi Saitoh and two anonymous reviewers for commenting on the manuscript. This study was financially supported by Tropenbos, Utrecht University and the Forest Science Institute of Vietnam.

References

Achard F, Eva HD, Stibig HJ, Mayaux P, Gallego J, Richards T, Malingreau JP (2002) Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002

Batista WB, Platt WJ, Macchiavelli RE (1998) Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. Ecology 79:38–53

Bawa KS, Ashton PS (1991) Conservation of rare trees in tropical rain forests: a genetic perspective. In: Falk DA, Holsinger KE (eds) Genetics and conservation of rare plants. Oxford University Press, Oxford, pp 62–71

Bierzychudek P (1999) Looking backwards: assessing the projections of a transition matrix model. Ecol Appl 9:1278–1287

Caswell H (2001) Matrix population models, 2nd edn. Sinauer Associates, Sunderland

Chien, PD (2006) Demography of threatened tree species in Vietnam. PhD thesis. Utrecht University, The Netherlands

Cochran EM, Ellner S (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. Ecol Monogr 62:345–364

de Kroon H, van Groenendael J, Ehrlen J (2000) Elasticities: a review of methods and model limitations. Ecology 81:607–618

Dowe J L, Benzie J, Ballment E (1997) Ecology and genetics of *Carpoxylon macrospermum* H. Wendl. and Drude (Arecaceae), an endangered palm from Vanuatu. Biol Conserv 79:205–216

Floyd SK, Ranker TA (1998) Analysis of a transition matrix model for *Guara neomexicana* spp. *coloradensis* (Onagraceae) reveals spatial and temporal demographic variability. Int J Plant Sci 159:583–563

Fox GA, Gurevitch J (2000) Population numbers count: tools for near-term demographic analysis. Am Nat 156:242–256

Franco M, Silvertown J (2004) Comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538

Harvey HF (1985) Population biology and the conservation of rare species. In: White J (ed) Studies in plant demography: Fetschrift for John L. Harper. Academic Press, Orlando, pp 111–123

Hiep NT, Loc PK, Luu NDT, Thomas PI, Farjon A, Averyanov L, Regalado Jr J (2004) Vietnam conifers conservation status review. Labour and Society Publisher, Hanoi

Horvitz CC, Schemske DW (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb—projection matrix analysis. Ecol Monogr 65:155–192

Hung TV (2004) Forestry research for the coming time. J Agric Rural Dev 12:26–29

Keith DA (2000) Sampling designs, field techniques and analytical methods for systematic plant populations surveys. Ecol Manage Restor 1:125–139

Keo HV (2003) Research on ecological—characteristics and reproductive capability by cutting of *Dacrydium elatum* (Roxb.) Wallich ex Hook in Bach Ma National Park. PhD thesis. Hue Science University, Hue

Kwit C, Horvitz CC, Platt WJ (2004) Conserving slow-growing, long-lived tree species: input from the demography of a rare understory conifer, *Taxus floridana*. Conserv Biol 18:432–443

Lande R (1988) Genetic and demography in biological conservation. Science 241:1455–1460

Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am Nat 142:911–927

Menges ES (1992) Stochastic modeling of extinction in plant population. In: Fiedler PL, Jain SK (eds) Conservation biology: the theory and practice of nature conservation, presentation and management. Chapman and Hall, New York, pp 253–276

Menges ES (2000) Population viability analyses in plants: challenges and opportunities. Trends Ecol Evol 15:51–56

Ministry of Science, Technology and Environment (MSTE) (1996) Red data book of Vietnam, vol 2—plant. Science and Techniques Publisher, Hanoi

Nghia NH (2000) Some threatened tree species of Vietnam. Agriculture Publisher, Hanoi

Oostermeijer JGB, Luijten SH, Den Nijs JCM (2003) Integrating demographic and genetic approaches in plant conservation. Biol Conserv 113:389–398

Peres CA, Baider C, Zuidema PA, Wadt LHO, Kainer KA, Gomes-Silva DAP, Salomao RP, Simoes LL, Franciosi ERN, Valverde FC, Gribel R, Shepard Jr GH, Kanashiro M, Coventry P, Yu DW, Watkinson AR, Freckleton RP (2003) Demographic threats to the sustainability of Brazil nut exploitation. Science 302:2112–2114

Pico FX, Riba M (2002) Regional-scale demography of *Ramonda myconi*: remnant population dynamics in a preglacial relict species. Plant Ecol 161:1–13

Poorter L, Bongers F, van Rompaey RSAR, de Klerk M (1996) Regeneration of canopy tree species at five sites in West African moist forest. For Ecol Manage 84:61–69

Schemske D, Husband BB, Ruckelshaus M, Goodwillie C, Parker I, Bishop G (1994) Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584–606

Silvertown J, Franco M, Menges M (1996) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conserv Biol 10:591–597

Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol 19:654–660

Thu NB, Can VV (1999) Cho Dai tree (*Annamocarya sinensis*). Agriculture Publisher, Hanoi

Van Mantgem PJ, Stephenson NL (2005) The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. J Ecol 93:737–747

Wang D-L, Li Z-C, Hao G, Chiang T-Y, Ge X-J (2004) Genetic diversity of *Calocedrus macrolepis* (Cupressaceae) in southwestern China. Biochem Syst Ecol 32:797–807

Whitmore TC (1997) Tropical forest disturbance, disappearance, and species loss. In: Laurance WR, Bierregaard RO (eds) Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago, pp 3–12

World Conservation Union (IUCN) (2006) The IUCN red list of threatened species. Available from http://www.redlist.org/info/tables/table6a. Accessed Dec 2007

Yao X, Ye Q, Kang M, Huang H (2007) Microsatellite analysis reveals interpopulation differentiation and gene flow in the endangered tree *Changiostyrax dolichocarpa* (Styracaceae) with fragmented distribution in central China. New Phytol 176:472–480

Zeide B (1993) Analysis of growth equation. Forest Sci 39:594–616

Zuidema PA, Franco M (2001) Integrating vital rate variability into perturbation analysis: an evaluation for matrix population models of six plant species. J Ecol 89:995–1005

Zuidema PA, Boot RGA (2002) Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. J Trop Ecol 18:1–31