

REVIEW

What do matrix population models reveal about the sustainability of non-timber forest product harvest?

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Summary

1. Understanding how management activities impact plant population dynamics is necessary to conserve at-risk species, control invasive species and sustainably harvest non-timber forest products (NTFP). For NTFP, knowledge about how the sustainability of harvest varies by plant life-form and part harvested is limited and needed to inform management of the thousands of species providing income to millions of people world-wide.

2. Matrix population models are commonly used to generate management recommendations. We reviewed studies of 46 NTFP species that used matrix models and synthesize the current knowledge on harvest effects. For 19 species with harvested and control populations, we assessed the impacts of harvest on projected population growth rates (λ) using meta-analysis and analysed trends in population responses to harvest across species, life-forms and plant part harvested using elasticity and life table response experiment (LTRE) analyses, and the combination of both, to assess vulnerability to harvest.

3. NTFP harvest significantly reduced λ across species. On the scale of individual studies, however, λ provided little information about harvest sustainability unless replication was sufficiently high. Most studies had low levels of replication over space or time and did not include contrasting levels of harvest.

4. Whole-plant harvest of herbs and bark harvest from trees were not sustainable largely because of decreases in survival. Palm leaf or fruit harvest and rattan stem harvest were potentially sustainable. Combined elasticity–LTRE analysis was especially valuable in assessing the sustainability of harvest when differences in λ between harvested and control populations were small, for studies with limited replicates, and where harvest effects varied regionally.

5. *Synthesis and applications.* The use of matrix models to assess the impacts of NTFP harvest is still rare in regions where trade of wild plants is heaviest and for several commonly harvested life-forms. Given the high variance in estimates for most NTFP species, λ does not provide a precise assessment of harvest impacts. We recommend that managers consider the combined elasticity–LTRE analysis in addition to λ in making management decisions for NTFP. NTFP research that accounts for environmental drivers of population dynamics in addition to harvest should be prioritized.

Key-words: conservation, demography, elasticity analysis, extraction, life table response experiments, management, meta-analysis, review

Introduction

Ecological studies aimed at determining the impacts of management activities on plant population dynamics are critical

to the conservation of rare and endangered species, eradication of invasive species and sustainable harvest of non-timber forest products (NTFP). The ultimate goals of such studies are to understand and predict the effects of management and to recommend strategies to increase population growth rates of at-risk or harvested species, or decrease population growth rates of invasive species. In the case of NTFP, which are an important source of income for millions of people around the

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world, management recommendations often aim to promote sustainable harvest as a way to conserve the harvested species and habitat while supporting local livelihoods (Hall & Bawa 1993). The accuracy of these recommendations is of vital importance: overly conservative management recommendations can deprive people of important sources of income, medicine or culturally valuable plants, while inappropriate management decisions can threaten population viabilities and endanger species.

A growing number of studies have assessed the effects of NTFP harvest on population dynamics (Pinard 1993; Bernal 1998; Ticktin *et al.* 2002, Ticktin 2004; Ghimire *et al.* 2008; Gaoue & Ticktin 2010), but a comparative analysis of these studies is still missing. Given that thousands of NTFP species are harvested, there are clear limitations to acquiring long-term data on population dynamics and harvesting impacts for most of these species. A synthesis of the literature on NTFP demography can provide insight on the potential for NTFP sustainability by identifying trends in responses to harvest. Such synthesis can provide management guidelines for NTFP species that may not have been studied and can improve our ability to efficiently use the limited resources available for research into NTFP management and conservation. This analysis can also point to existing gaps in the literature and provide insight on experimental designs that may be most appropriate to assess the effects of NTFP management. The latter also holds relevance for evaluating other kinds of management activities, including those aimed at at-risk or invasive species.

The most common approach to assessing the impacts of NTFP harvest on population dynamics has been the use of matrix population models (Caswell 2001). In these studies, stage-based matrix models are built from repeated measures of vital rates (survival, growth and reproduction) of individual plants. From these data, population growth rates (λ) are calculated to assess whether, over the long-term, a population is expected to grow, remain stable or decline under current conditions. For harvested populations, $\lambda \geq 1$ is usually interpreted to reflect a sustainably harvested population, whereas $\lambda < 1$ is interpreted to reflect unsustainable harvest (Bernal 1998; Svenning & Macía 2002; Endress, Gorshov & Berry 2006).

In addition to λ , elasticity analyses (Caswell 2001) are commonly used to predict the effects of NTFP harvest and suggest management strategies to reduce harvesting impacts (Ratsirarson, Silander & Richard 1996; Anderson & Putz 2002; Freckleton *et al.* 2003; Guedje *et al.* 2007). Elasticity analyses project how λ would change in response to small changes in population vital rates. For example, a small change in a vital rate with high-elasticity values will have a big impact on λ ; similarly, changes in vital rates with low elasticity will lead to very small changes in λ . A related approach, life table response experiments (LTRE) (Caswell 2001), has been used to assess how observed differences in rates of survival, growth and reproduction between harvested and unharvested populations contributed to observed differences in λ (Ghimire *et al.* 2008; Farrington *et al.* 2009; Gaoue & Ticktin 2010). Vital rates with

high LTRE contributions make the biggest contributions to the observed differences in λ between harvest and control populations.

Considering the results of both elasticity and LTRE analyses is a well-known approach to understanding processes underlying population dynamics and designing conservation and management recommendations for plant species (Horvitz & Schemske 1995), including NTFP (Ghimire *et al.* 2008). Zuidema, de Kroon & Werger (2007) proposed a novel approach that combines these two analyses to provide a more robust tool to assess the sustainability of NTFP. This approach identifies vital rates whose change because of harvest had the greatest effect on λ (based on LTRE contributions) and evaluates the potential impacts of these changes on λ (based on elasticity values). When high-elasticity vital rates have low LTRE contributions, and therefore contribute little to differences in λ between harvested and unharvested populations, harvest is potentially sustainable. Similarly, when harvest-mediated differences in λ (LTRE contributions) are due to vital rates with low elasticity, there is potential for sustainable harvesting, as the vital rates that most affect λ are not affected by harvest (Zuidema, de Kroon & Werger 2007). In contrast, when high-elasticity vital rates also have high negative LTRE contributions, harvest is expected to have a significant impact on population growth and a low chance of sustainability. Zuidema, de Kroon & Werger (2007) applied this combined analysis to three understory palm species harvested for leaves, but this approach is yet to be extended to other NTFP species harvested for other plant parts or with different life histories.

In this study, we use a meta-analysis to assess the impacts of NTFP harvest on population growth rates (λ) and apply the approach of Zuidema, de Kroon & Werger (2007) to a larger sample of plant species from different life-forms and harvest types. We address the following questions: (i) What is the scope of studies to date that use matrix models to assess the impacts of NTFP harvest? (ii) Are there trends in population responses to harvest across species? (iii) What is the potential for sustainable harvest of NTFP species, life-forms and harvested parts? (iv) What are the priorities for future research on NTFP species demography?

Materials and methods

DATA ACQUISITION

We searched several databases (Web of Science, Science Direct, Google Scholar and ProQuest Dissertations & Theses) for papers and dissertations which used matrix population models to investigate the impacts of NTFP harvest on population dynamics. We used the following keywords in the search: 'non-timber forest products', 'lambda', 'matrix modeling', 'Caswell', 'plant harvest', 'population dynamics' – and variations (e.g. 'non-timber', 'NTFP'). To identify trends in the effects of NTFP harvest on population dynamics, we selected studies that included populations that were harvested during the study period and control populations. Control populations either had no harvest or else very low levels of harvest (as in Ghimire *et al.* 2008; Gaoue & Ticktin 2010). We extracted the published population projection matrices

from each study or obtained them from study authors, compiling 134 matrices in total.

EFFECT OF HARVEST ON POPULATION GROWTH RATES

Matrix models take the form of $n(t + 1) = A * n(t)$, where $n(t)$ and $n(t + 1)$ are vectors representing the number of individuals in each stage (or size class) at times t and $t + 1$, and A is the projection matrix containing the probabilities of transitions among stages between time periods (1 year in all studies). Element a_{ij} of matrix A represents the number of individuals in stage i per individual in stage j in the previous year. We calculated λ , which is the dominant eigenvalue of A and represents the asymptotic population growth rate. When necessary, we added values of 0.001 to published transitions to meet assumptions of matrix irreducibility (Caswell 2001). We used the *popbio* package (Stubben & Milligan 2007) in R (R Development Core Team 2010) to carry out all matrix analyses.

We performed a quantitative meta-analysis including species for which it was possible to estimate the mean and variation in λ for harvested and control populations, calculated from values of λ for each species from multiple populations and/or across multiple years for each treatment. For one species, we used the variance in λ reported by the authors (Guedje *et al.* 2007). We used the mean and standard deviation of the natural log of λ to calculate Hedges' d (Hedges & Olkin 1985), a metric of effect size that estimates the mean difference of the response variable between treatments (harvested vs. control), standardized by the pooled standard deviation of the response variable and corrected for small sample sizes (see Appendix S1, Supporting information).

We tested the hypothesis that harvest reduces λ by using a random effects model to calculate the mean and 95% confidence interval of effect size across species. The random effects model assumes that there is a true random component of variation in effect size between species in addition to sampling error (Rosenberg, Adams & Gurevitch 2000). The confidence interval for the mean effect size was calculated using bootstrap resampling with 4999 iterations. We rejected the null hypothesis of no effect of harvest on λ if the 95% bias-corrected bootstrap confidence interval for effect size did not overlap zero.

We calculated Rosenberg's $N + 1$ fail-safe number (Rosenberg 2005) to estimate the number of studies of null effect and mean weight that would need to be added to our meta-analysis to reduce the significance of the cumulative effect size to 0.05 (Rosenberg, Adams & Gurevitch 2000). A fail-safe number $> 5n + 10$, with n being the number of studies included in the meta-analysis, indicates that the results of the analysis are robust to potential publication bias (Rosenthal 1991). All calculations for the meta-analysis were carried out in MetaWin 2.1 (Rosenberg, Adams & Gurevitch 2000).

ELASTICITY AND LTRE ANALYSIS – LOOKING BEYOND λ

For all populations of each species, we calculated the elasticity of λ to proportional change in vital rates rather than to changes in matrix elements a_{ij} (Franco & Silvertown 2004). We calculated vital rate elasticities as:

$$\frac{x}{\lambda} \frac{\partial \lambda}{\partial x} = \frac{x}{\lambda} \sum_{ij} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}$$

where x is the vital rate and a_{ij} is the matrix transition from stage j to stage i . Unlike transition elasticities, vital rate elasticities do not necessarily sum to 1 and can be negative or positive (Caswell

2001). For each species, we used fixed-effect LTREs (Caswell 2001) to estimate the contributions of vital rates to differences in λ between harvested vs. control populations. Within studies, we used paired comparisons between harvested and control populations within years and additional factor levels (e.g. region, site) when possible. For species exposed to multiple levels of harvest, we compared each harvesting level with the control population. When paired comparisons between single populations were not possible, we calculated a mean matrix per treatment across populations by averaging vital rates and conducted LTREs by year and region, where applicable. For one species (*Saussurea medusa*), asynchronous seedling recruitment between treatments across years meant that comparisons within years were not informative. In this case, we averaged matrices across years per treatment and conducted a single LTRE. We calculated LTRE contributions summed by vital rate type. For example, the LTRE contribution of survival equals

$$\sum_j (s_j^{(h)} - s_j^{(c)}) \frac{\partial \lambda}{\partial s_j} |_{A^{(m)}}$$

where $s_j^{(h)}$ is the survival of stage j in the harvested matrix, and $s_j^{(c)}$ is the survival of stage j in the control matrix. $\partial \lambda / \partial s_j$ is the sensitivity of λ to the survival of stage j evaluated at the midway matrix $A^{(m)}$. We used midway sensitivities based on matrices constructed from the mean vital rates of the matrices being compared.

To assess the potential for sustainable harvest, we used combined prospective–retrospective analysis (Zuidema, de Kroon & Werger 2007) and plotted the LTRE contributions against the elasticities of each vital rate of control populations. We examined plots to determine whether or not high-elasticity vital rates also had high LTRE contributions.

Results

DIVERSITY AND DISTRIBUTION OF NTFP STUDIES USING MATRIX MODELS

We found studies with data from 46 species across 20 families that used matrix models to assess the effects of NTFP harvest (see Table S1, Supporting information). One-third of studies (16 spp.) monitored only unharvested populations and simulated harvest effects, whereas about one-fifth (10 spp.) lacked control populations.

Nearly half the species were palms (21 spp.). Trees (12 spp.) and herbs (12 spp.) each represented approximately one-quarter of the species. There was a single study of a cycad species. The palm species were harvested mainly for their leaves or stems. Trees were harvested for fruit, seeds, bark, leaves or resinous wood. Most studied herbs were harvested for their roots or rhizomes, which often results in the death of the whole plant. Seventy-three per cent of species studied are of tropical origin.

For 20 of the 46 species we found, the impacts of harvest were evaluated from both harvested and control populations; 75% of these studies were published since 2005. As matrices were not available for one species, we carried out further analyses using data from 19 NTFP species with harvested and control populations. The great majority of species in

Table 1. Non-timber forest products species with demographic data from both harvested and control populations

Species	Family	Life-form	Plant part harvested	Study	Habitat	No. pops. ^a	No. years
<i>Aechmea magdalenae</i>	Bromeliaceae	Monocarpic herb	Leaves, ramets or whole plant	Ticktin <i>et al.</i> (2002)	Tropical rain forest, Mexico	2/4	2–3
<i>Agave marmorata</i>	Agavaceae	Monocarpic herb	Stems, inflorescence	Jimenez-Valdes <i>et al.</i> (2010)	Tropical deciduous forest, Mexico	2/2	2
<i>Echinacea angustifolia</i>	Asteraceae	Herb	Roots	Hurlburt (1999)	Temperate prairie, US	4/4	2
<i>Linonitum carolinianum</i> ^b	Plumbaginaceae	Herb	Flowers	Baltzer <i>et al.</i> (2002)	Saltmarsh, Canada	0/1	3
<i>Nardostachys grandiflora</i>	Valerianaceae	Herb	Rhizome	Ghimire <i>et al.</i> (2008)	Temperate rocky-outcrop & meadow, Nepal	5/6	3
<i>Panax quinquefolius</i>	Araliaceae	Herb	Root	Mooney (2007)	Temperate deciduous forest, US	18/6	2–4
<i>Saussurea laniceps</i>	Asteraceae	Monocarpic herb	Plant	Law (2007)	Temperate alpine cliffs, Tibet/China	6/6	4
<i>Saussurea medusa</i>	Asteraceae	Monocarpic herb	Plant	Law (2007)	Temperate alpine cliffs, Tibet/China	6/6	2
<i>Syngonathus nitens</i>	Eriocaulaceae	Herb	Scapes	Schmidt (2011)	Tropical wet grassland/savanna, Brazil	12/12	1
<i>Astrocaryum mexicanum</i> ^b	Arecaceae	Palm	Leaves	Mendoza, Pintero & Sarukhan (1987)	Tropical rain forest, Mexico	0/2	6
<i>Calamus rhabdocladius</i> ^b	Arecaceae	Rattan palm	Stem	Binh (2009)	Tropical rain forest, Vietnam	0/2	2–3
<i>Chamaedorea elegans</i>	Arecaceae	Palm	Leaves	Valverde, Hernandez-Apolinar & Mendoza-Amaro (2006)	Tropical rain forest, Mexico	3/3	2
<i>Chamaedorea radicalis</i>	Arecaceae	Palm	Leaves	Endress, Gorchoy & Berry (2006)	Tropical cloud forest, Mexico	4/4	5
<i>Daemonorops cf. poilanei</i> ^b	Arecaceae	Rattan palm	Stem	Binh (2009)	Tropical rain forest, Vietnam	0/2	2–3
<i>Geonoma deversa</i>	Arecaceae	Palm	Leaves	Zuidema, de Kroon & Werger (2007)	Tropical rain forest (Amazon), Bolivia	2/2	2
<i>Mauritia flexuosa</i>	Arecaceae	Palm	Fruit	Sampaio & Santos unpublished data	Tropical swampy forest/savanna, Brazil	5/5	1
<i>Garcinia lucida</i> ^b	Clusiaceae	Tree	Bark	Guedje <i>et al.</i> (2007)	Tropical rain forest, Cameroon	1/1	1
<i>Khaya senegalensis</i>	Meliaceae	Tree	Bark and leaves	Gaoue & Ticktin (2010)	Tropical savanna, Benin	11/11	2
<i>Prunus africana</i> ^b	Rosaceae	Tree	Bark	Stewart (2001)	Tropical rain forest, Cameroon	4/4	2

^aThe total number of control and harvested populations from the study included in our analysis. The first number is the populations included in the meta-analysis and the second number is the populations included in the LTR.

^bStudies applied harvest to target-stages only. Harvest matrices were calculated by combining data from non-target control individuals with targeted harvested individuals.

each life-form were harvested for the same parts: herbs harvested for roots or rhizomes, palms for leaves and trees for bark (Table 1; see Table S2, Supporting information). Data for 15 species contained estimates of variance in λ for harvested and control populations and were included in our meta-analysis.

EFFECTS OF NTFP HARVEST ON POPULATION GROWTH RATES AND VITAL RATE ELASTICITIES

Across species, harvest significantly reduced projected population growth rates ($d = -0.9427$, 95% CI = -1.6179 to -0.3877 ; Fig. 1). This is equivalent to a λ of 1.04 in control populations compared to 0.92 in harvested populations, calculated according to Lipsey & Wilson (2000). The fail-safe number was 91.11 indicating that our findings are robust to potential publication bias.

Among control populations, elasticity patterns follow those expected from plant life-form (Franco & Silvertown 2004). On average, the elasticity of λ to perturbations of survival was greatest in the long-lived palm and tree species and lowest in herbs (Fig. 2). Elasticities of λ to perturbations in growth were slightly higher among herbs than for other life-forms.

Harvest altered the patterns of elasticities for growth and fertility (Fig. 2). Harvest consistently decreased the elasticities of growth and fertility for palms and decreased the elasticity of growth for the trees, especially *Prunus africana*. For *Khaya senegalensis*, the impact of harvesting foliage and bark on elasticities varied by region: harvest decreased the elasticity of growth and fertility in the moist region, but had very little impact on elasticities in the dry region. For both palms and trees, the elasticity of survival was similar between harvested and control populations. The effects of harvest on the elasticities of herbs were mixed, varying both within and among species.

EFFECTS OF NTFP HARVEST BASED ON LTRE AND COMBINED ELASTICITY-LTRE

The contribution of vital rates to observed differences in λ between harvested and control populations differed by life-form and plant part harvested (Fig. 3). Among the herbs for which harvest causes mortality, decreased growth and survival were the biggest negative contributors to reduced population growth rates for *Agave marmorata*, *Saussurea medusa*, *Echinacea angustifolia*, *Nardostachys grandiflora* and *Panax quinquefolius*. For the latter three species, the vital rates most affected by harvest had high elasticities and high negative LTRE contributions (Fig. 4). For *Limonium carolinianum*, reductions in fertility from flower harvest had the most negative LTRE contributions.

Declines in reproduction contributed most to the reduction in λ from leaf harvest of palm species. In the case of *Geonoma deversa*, which can reproduce clonally, small positive contributions from increased ramet growth were cancelled out by greater negative contributions from decreased growth of genets. For *Chamaedorea elegans*, negative contributions from reduced fertility were partially offset by positive contributions from survival. The combined elasticity-LTRE analysis indicates that vital rates with high elasticities were rarely affected by palm leaf harvest, except at very high harvesting intensities. For the two stem-harvested rattans, during the year of harvest, the largest negative LTRE contributions were from decreased survival, the highest elasticity vital rate.

Overall, reductions in rate of survival contributed most to the observed reduction in λ by bark harvest for the three bark-harvested tree species. However, the impact of harvest differed by region for *K. senegalensis*. In the drier region, the impact of harvest resulted almost entirely from reduced survival. In the wetter region, reduced fertility contributed most to the reduced

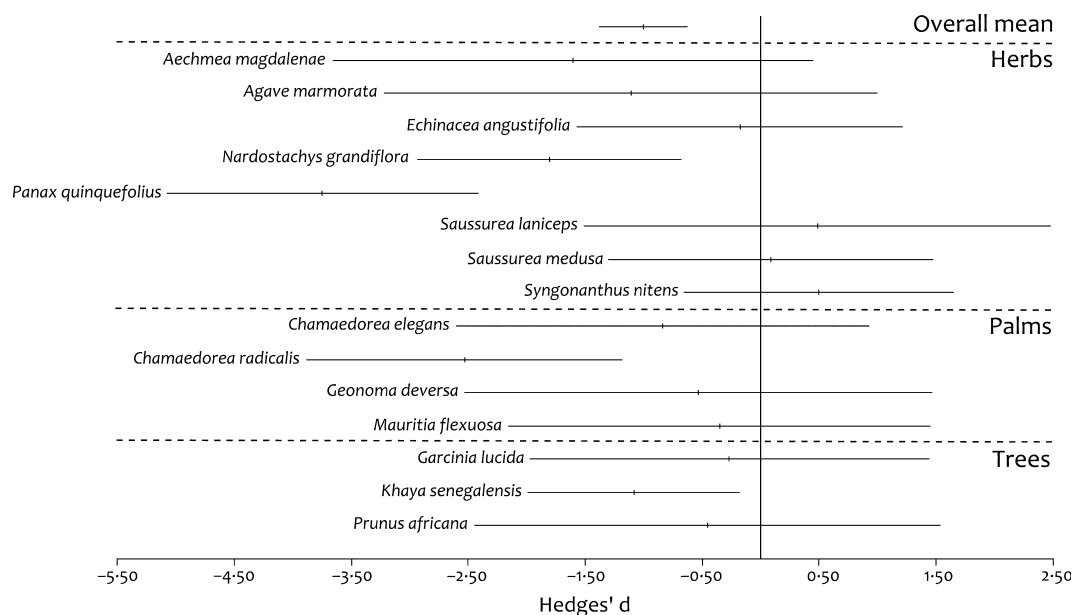


Fig. 1. There is a significant effect of harvest on projected population growth rates [$\ln(\lambda)$] across 15 non-timber forest product species. When considered individually, only four studies – including two herbs, one palm, and one tree – show a significant decline in projected growth rates in harvested populations.

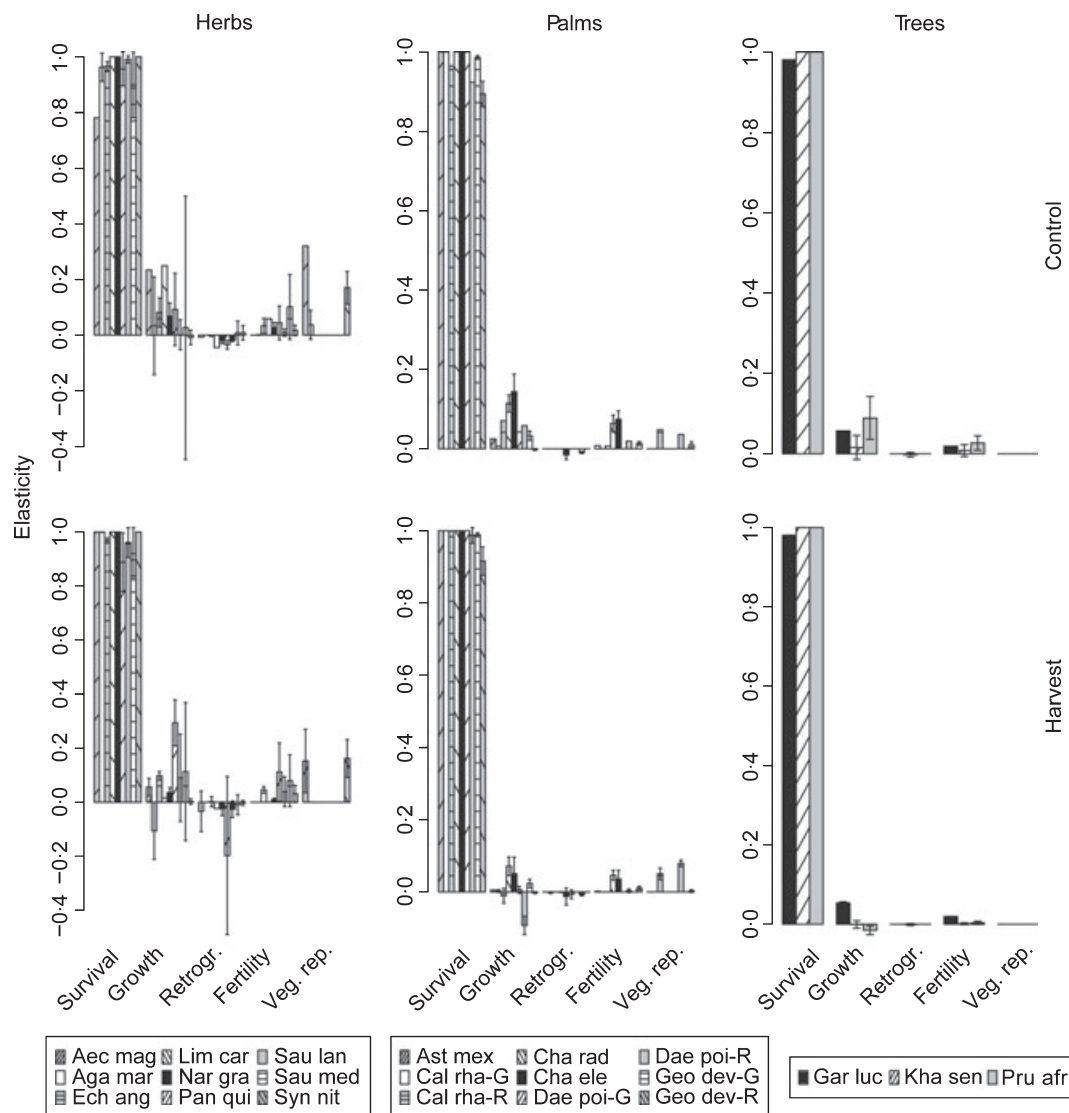


Fig. 2. Vital rate elasticities of non-timber forest products species differ among life-forms, as well as between harvested and control populations. Unpublished data from *Mauritia flexuosa* showed a similar pattern to the other palms, but has been omitted from Figs 2–4 at the request of the authors. For species with multiple control and harvested populations, mean elasticity values and standard deviations are presented. For *C. rhabdocladus*, *G. deversa* and *D. cf. poilanei* elasticity values for genets (G) and ramets (R) are shown separately.

population growth rate. For *Prunus africana* and *Khaya senegalensis*, which are harvested for their bark, survival rates had high LTRE contributions and also high-elasticity values.

Discussion

WHAT IS THE SCOPE OF NTFP MATRIX-MODELLING STUDIES TO DATE?

The number of studies that use matrix population models is limited with respect to the thousands of NTFP species. There are many NTFP-rich regions with heavy trade of wild plants that are missing or underrepresented. For example, studies of tropical NTFP species are heavily concentrated in Latin America, while studies of African and Asian plants species are rare, even though the number of commercially harvested species in

these regions is high (Schippmann, Leaman & Cunningham 2006). In temperate zones, most NTFP studies are limited to the United States and Canada. It is worth noting the complete absence of NTFP matrix-modelling studies in Australia and Europe, despite the heavy wild harvest of medicinal plants in Eastern Europe (Schippmann, Leaman & Cunningham 2006). The lack of studies that include both harvested and control populations of lianas, vines, ferns, mosses, lichens and cycads, all of which are common NTFP, highlights the need for more studies on these life-forms especially.

Most studies did not directly compare harvested and control populations. Although the availability of unharvested populations is frequently assumed to be a limiting factor for NTFP research, our finding that one-third of studies were based only on unharvested populations suggests that is often not the case. For these cases, including experimental harvest instead of

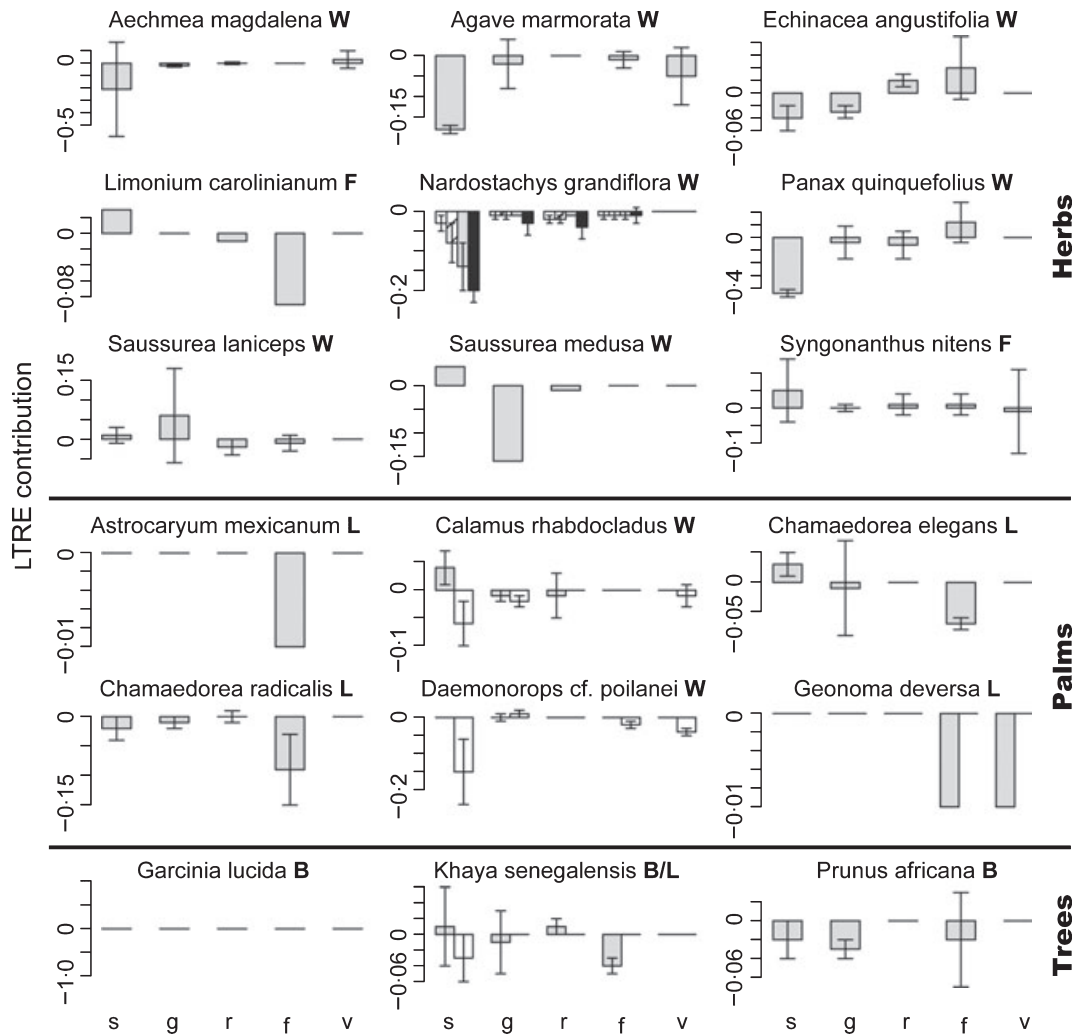


Fig. 3. Vital rate LTRE contributions (survival, growth, retrogression, fertility and vegetative reproduction) to the effect of harvest differ among non-timber forest products species: herbs, palms and trees. For *N. grandiflora*, bars represent increased levels of harvesting intensity (10, 25, 50 and 75%). For *C. rhabdocladus*, *G. deversa* and *D. cf. poilanei*, grey bars are ramet contributions and white bars are genet contributions. For *Khaya senegalensis*, grey bars represent the wetter Sudano-Guinean region and white bars represent the drier Sudanian region. The scale of the y axis varies by species. Letters in bold after the species name indicate plant part harvested: W for harvest that may cause whole-plant death, F for flowers and flower stalks, L for leaves and B for bark harvest.

relying on simulations could greatly contribute to understanding the impacts of harvest. Those studies that did compare harvested to control populations were restricted in their replication in space and time. With some exceptions (Endress, Gorchov & Berry 2006; Gaoue & Ticktin 2010), most studies were shorter than 3 years, included fewer than five populations, and were restricted to a small geographic region.

EFFECTS OF NTFP HARVEST ON λ

Our finding that harvest significantly decreases λ confirms that the potential for unsustainable harvest constitutes a serious threat and an important management consideration for NTFP species. The number of studies within life-form categories was too low to test for differences in harvesting effect among life-forms. From a management perspective, it is important to understand the effects of harvest on individual species. Here,

only four species (*Chamaedorea radicalis*, *Khaya senegalensis*, *Nardostachys grandiflora* and *Panax quinquefolius*) exhibit statistically significant effect sizes within a study (Fig. 1). For *C. radicalis*, the very high harvesting levels were responsible for the negative impact, whereas low harvesting levels do not decrease λ significantly (Endress, Gorchov & Berry 2006). For the other 11 species, as the wide confidence intervals for effect sizes show, it is impossible to determine whether there truly is no biologically significant effect of harvest for these species, or whether the study simply failed to detect an effect. For four of the eight herbaceous species (*Echinacea angustifolia*, *Saussurea laniceps*, *Saussurea medusa* and *Syngonanthus nitens*), the differences between harvested and control populations varied greatly among sites and years. For the two *Saussurea* species and *Syngonanthus nitens*, the positive effect of harvest on population growth rates reported may be in fact because of temporal and spatial variation, respectively.

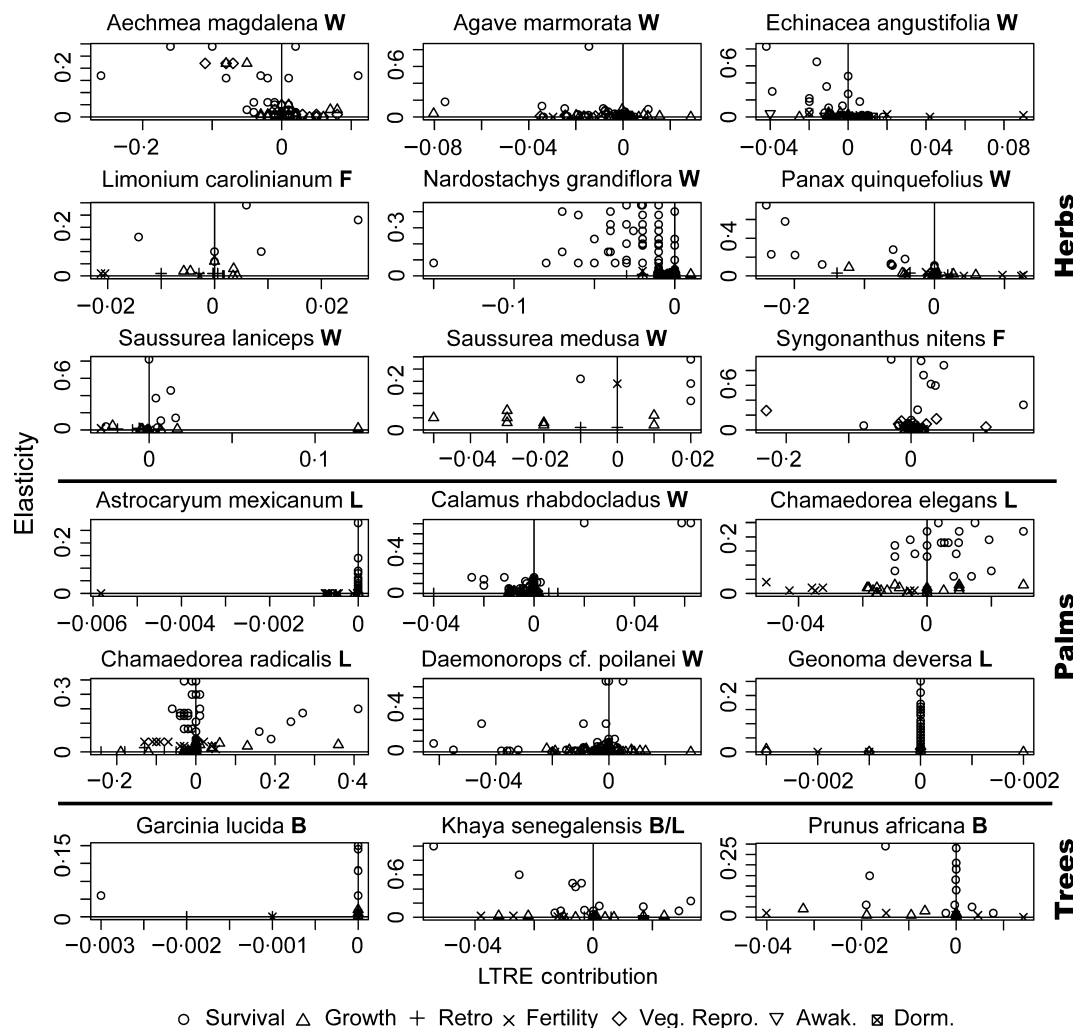


Fig. 4. The contribution of vital rates (survival, growth, retrogression, fertility, vegetative reproduction, awakening and dormancy) to the harvesting effect (LTRE contributions) relative to vital rate elasticities for the non-timber forest product species considered in this review. Vital rates that have either low elasticities and/or low LTRE contributions (occurring along the axes) suggest potentially sustainable harvest. Vital rates with high negative elasticities and high LTRE contributions suggest the potential for unsustainable harvest. Each point represents a vital rate for a single size class. The scale of the axes varies by species. Letters in bold after the species name indicate harvest type: W for harvest that may cause whole plant death, F for flowers and flower stalks, L for leaves and B for bark harvest.

The high within-study variance in estimates of λ illustrates the challenge of assessing the sustainability of harvest using only λ or changes in λ . Because harvested populations are concurrently subject to other sources of environmental variation and disturbance unrelated to harvest, it can be difficult to determine conclusively whether there is an effect of harvest on λ , and, in cases where harvested populations are declining, to what degree harvest is actually a contributing factor (Ticktin 2004; Gaoue & Ticktin 2008). Determining the impacts of harvest for herbaceous species may be especially challenging because of their sensitivity to variation in microhabitat (Godefroid, Rucquoi & Koedam 2006). Our finding that environmental variation was often stronger than and/or confounded with the effects of harvest is consistent with other studies that have found environmental variation to have a significant impact on population dynamics and exacerbate harvesting impacts (Martinez-Ramos, Anten & Ackerly 2009). This is problematic because, in contrast to other conservation

research, most NTFP harvest studies tend to interpret λ literally (Crone *et al.* 2011), and therefore, management decisions based on conclusions from these studies may be inappropriate. Our results emphasize that management decisions for NTFP should not be based on λ values alone.

In addition to life-form and part harvested, the responses to harvest observed in the 19 species considered are also influenced by harvest history, harvest intensity and harvesting interval. Because of the variation among studies, we were unable to assess the impact of these additional factors, but they are undoubtedly worthy of further examination.

ASSESSING THE POTENTIAL FOR SUSTAINABLE HARVEST USING COMBINED ELASTICITY-LTRE

Our results illustrate trends in the sustainability of NTFP harvest across life-forms and plant part harvested, though these two factors are correlated within existing studies. Combined

elasticity–LTRE analysis suggests that whole-plant harvest of many herb species is potentially unsustainable (Fig. 4). Harvest of *Echinacea angustifolia*, *Nardostachys grandiflora* and *Panax quiquefolius* reduces high-elasticity survival vital rates, limiting the potential for sustainable harvest. Similarly, reductions in high-elasticity rates of survival, growth and clonal reproduction make certain types of harvest of *Aechmea magdalenae* potentially unsustainable (Ticktin & Johns 2002).

It is worth noting that for some of the herbaceous species whose harvest entails mortality, *Echinacea angustifolia*, *Panax quiquefolius* and *Aechmea magdalenae*, we found positive LTRE contributions from fertility or vegetative reproduction in harvested populations, suggesting possible density-dependent responses at the population level (Fig. 3). The negative effect of harvest on λ was therefore not as great as would have been predicted from observing only unharvested populations and analysing elasticities. Identifying optimal densities for these species may improve the potential for sustainable harvest.

Similarly to Zuidema, de Kroon & Werger (2007), we found that leaf and fruit harvest are potentially sustainable for palms. In contrast, stem-harvested rattan species show some negative LTRE contributions from high-elasticity vital rates. However, these species' potential for regeneration is high, and high negative LTRE contributions are not found 2 years after harvesting, which indicates that the species can be resilient to harvest if enough time between harvests is allowed (Binh 2009).

The lack of large negative LTRE contributions for the bark-harvested tree, *Garcinia lucida*, suggests harvest is potentially sustainable – at least from an ecological perspective. However, as Guedje *et al.* (2007) note, while λ were largely unaffected by harvest, harvest leads to a replacement of large reproductive trees with small resprouts and strongly reduces the abundance of trees of harvestable size, and so may not be economically viable. Overall, bark harvest for the three tree species considered appears to be potentially unsustainable, or to require such low levels or long harvesting intervals as to be economically unviable.

Our results suggest that the combined elasticity–LTRE approach advocated by Zuidema, de Kroon & Werger (2007) provides valuable additional insights into the vulnerability of species to harvest in at least three cases. First, when there is little variation in λ between harvested and control populations, high LTRE contributions from transitions with high-elasticity values (e.g. *Echinacea angustifolia* and *Panax quiquefolius*) indicate that NTFP harvest is potentially unsustainable, even when current levels of harvest do not bring λ below one. If increased harvest levels or environmental stress reduce population growth rates, harvest may be enough to cause population declines.

Secondly, when the number of replicate populations is limited but different harvest levels are assessed, the elasticity–LTRE approach provides insights on the effects of harvest, independent of other disturbances. For example, in the case of *Nardostachys grandiflora* (Ghimire *et al.* 2008), the highest LTRE contributions resulted from changes in survival rates, the vital rate with highest elasticity values, which suggests low

sustainability. Although this study included only one population per harvest level, the consistent decrease in λ and the consistent increase in the negative LTRE contributions of survival and growth as harvesting intensity increased strongly suggests that patterns are because of harvest rather than other environmental variation.

Thirdly, when the effects of harvest vary across the landscape, as for *Khaya senegalensis*, combined elasticity–LTRE highlights how the potential for sustainable harvest may vary with environmental conditions (Gaoue & Ticktin 2010). Management recommendations would therefore depend on the region where harvesting is occurring – even when differences in λ are not necessarily apparent. A recent study of three temperate short-lived perennials found considerable variability in vital rates among regions, and that spatial variation was greater than temporal variation (Jongejans *et al.* 2010). The impacts of harvest are likely to be quite variable for many other NTFP species that are harvested across large geographic and climatic ranges.

However, as is the case with λ values, combined elasticity–LTRE analysis of NTFP populations may be uninformative or – if misinterpreted – misinformative, when spatial and/or temporal variation is high and replication is low, so that the effects of harvest cannot be distinguished from other forms of environmental variation. For example, in the case of the two *Saussurea* species, seed germination was highly variable between years. Because reproduction in the harvested and unharvested populations of *Saussurea medusa* was not synchronized, differences in λ between treatments within years depended on which populations were reproducing at that time, rather than on harvesting treatment. It would be misleading to interpret these differences as an effect of harvest. The potential for drawing erroneous conclusions about the impacts of harvest relative to other sources of variation is especially likely when estimates of variation among populations with similar harvest levels are lacking. When we compare the pooled matrices for harvested and unharvested *Syngonanthus nitens* populations, harvest appears to increase λ owing to a positive LTRE contribution from clonal reproduction. However, once we take into account spatial variation by comparing the paired harvested and unharvested populations (six sites with both treatments each), it becomes clear that the increases in λ and clonal reproduction are not consistently related to harvest.

RECOMMENDATIONS FOR FUTURE NTFP STUDIES

One of the most apparent results of our analysis is the high variation in demographic parameters and estimates of growth rates of NTFP populations over space and time, regardless of harvest. As a result, researchers and managers must carefully assess the most effective means of generating management decisions for each NTFP species. For example, studying the dynamics of one or a few harvested NTFP populations over 2 years may provide little information about the effects of harvesting across the larger geographic and temporal scales at which harvest is likely occurring. For management, such a limited study may not be much more informative than considering

guidelines based on species life-form, plant part harvested and harvesting intensity, yet it would be much more costly and time intensive. On the other hand, making management decisions based solely on elasticity analyses of non-harvested populations, as is made in more than one-third of the 46 NTFP matrix model studies we reviewed, risks missing indirect and compensatory responses to harvest. Similarly, studies that employ experimental harvest at the level of the individual plants rather than at the population level, and those that average vital rates between harvested and control populations, will fail to identify potential indirect effects of harvest. Our finding that three of the eight herb species included in this analysis showed evidence of population-level compensatory responses suggests that these reactions may not be uncommon, at least for herbs.

An important way to test the direct effects of NTFP harvest is to take the potential for spatiotemporal variation into account in the study design. This can be done by

building matrix models from data from control and replicated harvest plots, carried out over several years, across the range of environmental conditions, harvest and management practices over which harvesting occurs. Long-term studies are important to capture the effects of temporal variation, as well as to determine the cumulative effects of harvest, especially for experimental harvests. Our results suggest that several replicates per harvest treatment and environmental context are probably necessary to identify how harvest is affecting populations. It is noteworthy that in our analysis, the four studies with a significant effect size of λ were the studies with the greatest number of replicates (Fig. 1 and Table 1). We recommend this strategy whenever possible, as these kinds of studies are necessary for deriving generalizations about the impacts of harvest. Replicates of harvested plots or populations can be obtained by experimental harvests by local harvesters, by monitoring existing

Table 2. Summary of non-timber forest products research recommendations. Study design types are listed in order of decreasing potential to produce robust recommendations for management decisions

Study design	Most useful for	Most relevant analyses for deriving management decisions	Benefits	Limitations
Multiple harvested and control populations Across species' environmental range Several years Different management practices/intensities	Whenever resources allow, and especially harvest with low potential for sustainability (harvest resulting in plant mortality, root and bark harvest)	λ , LTRE and elasticity	Distinguish between harvest effects and other environmental variation Assess sustainability of different forms of harvest Conclusions applicable across broad geographical area	Time intensive Possibly expensive Replicate populations necessary across multiple conditions
Multiple populations or plots under several levels of harvest One or more years	When multiple levels of harvest exist across a relatively homogenous environment	LTRE and elasticity	Possible to distinguish harvest effects from environmental variation Rapid assessment possible Fewer replicate populations required	Requires variation in harvesting intensities, experimental or observed Conclusions limited to narrow range of environmental conditions
One or a few populations, either harvested or control One or more years	When the above options are not possible	Elasticity	Rapid assessment possible Lower cost Possible with limited study populations and without variation in harvesting intensity	Effects of harvest on vital rates must be estimated with outside knowledge Cannot distinguish between effects of harvest and other sources of variation Conclusions limited to narrow range of environmental conditions

populations subject to harvest, or, ideally a combination both.

Another option is to collect data on environmental or management covariates that could potentially have an important effect on population dynamics (e.g. rainfall, fire, grazing). If these environmental drivers turn out to be important, they can be integrated into more complex matrix models of NTFP harvest (e.g. Menges & Quintana-Ascencio 2004), or used as covariates in integral projection models (Dahlgren & Ehrlén 2009; Hegland, Jongejans & Rydgren 2010).

However, for each of the thousands of NTFP species, these kinds of experiments often cannot be carried out. When experimental harvest is feasible but it is impossible to increase the number of replicates, we suggest an approach similar to Ghimire *et al.* (2008), where single study population or plots can be each be subject to a different intensity of harvest to determine whether changes in projected population growth rates or LTRE contributions show a directional trend consistent with increasing harvest intensity. This approach requires fewer replicates, resources and time and does not necessitate unharvested or even low-harvested populations. It can also either be applied experimentally or based on observed variation in harvested levels across populations. Of course, this also generates results that are restricted to the geographic scale and harvesting conditions studied (Table 2). This study design may also be beneficial to developing management plans for other plant species, and especially at-risk species where replicate study populations are limited and there is need for rapid decision-making.

Although this review only assessed the effects of NTFP harvest, the above recommendations are likely to be applicable to evaluating the effects of other kinds of management on plant populations, including those applied to rare or threatened species and to invasive species. Clearly, some general management decisions for NTFP can also be made directly, based only on life-form and plants part harvested. Our results and the existing literature strongly suggest that at least moderate levels of harvest is sustainable for perennials (excluding monocarps) harvested for reproductive structures, including fruit, seeds and flowers and palms harvested for their leaves. However, in some contexts, NTFP species may be declining because of environmental or management factors (aside from harvest). In those cases where populations are perceived to be in decline, studies using the approaches described above are key to identifying the most important drivers of decline. It is critical to determine whether harvest is an important driver of population decline because a decision to prohibit NTFP harvest can have large negative consequences for local livelihoods and of course may not lead to any increase in population size.

Our review of 46 NTFP species to which matrix models have been applied illustrates the necessity of carefully designing and interpreting studies of NTFP harvest. Given the significant overall negative impact of NTFP harvest on projected population growth rates, but a lack of a detectable effect within most species, we emphasize the importance of using combined elasticity–LTRE analyses to assess the potential for sustainable harvest. While the results we have synthesized provide a starting point for determining the potential for sustain-

able NTFP harvest, they represent a limited subset of life-forms and plant parts harvested world-wide. Additional appropriately designed studies are essential to increase our ability to understand the ecological impacts of harvest, generate research-based recommendations for management and promote sustainable use of NTFP species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Specifications on the meta-analysis methods.

Table S1. List and references of the 46 NTFP species considered in this review.

Table S2. List and characteristics of the 19 NTFP species used in the λ , elasticity, LTRE and meta-analyses.

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