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FORUM

Disentangling, again, the drivers of population decline for two harvested species: a response to Prasad *et al.* (2014)

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Summary

1. Ticktin *et al.* (2012) (*Journal of Applied Ecology*, **49**, 774) assessed the dynamics of two Indian tree species (*Phyllanthus emblica* and *P. indofischeri*) and showed that although fruit harvest can decrease long-term population growth rates (λ), the principal drivers of decline are mistletoe infestation and invasion of an exotic shrub. Prasad *et al.* (2014) (*Journal of Applied Ecology*, **51**, doi: 10.1111/1365-2664.12170) questioned Ticktin *et al.*'s approach, showed that *P. emblica* λ values increased when fruit harvest was banned and concluded that fruit harvest has a significant negative effect. We demonstrate that Prasad *et al.*'s analysis is fundamentally flawed and that our conclusions hold firm.

2. We clarify that our models are built from empirical data collected from field plots. We use life table response experiments to demonstrate that the increase in *P. emblica* λs after the fruit harvest ban is due to higher adult survival and unrelated to fruit harvest. *P. indofischeri* populations show no such increase.

3. We demonstrate that our results and the literature strongly back up our management recommendations to control mistletoe and the invasive shrub, and protect amla saplings.

4. *Synthesis and applications*. Prasad *et al.* (2014) confound the effects of time and treatment and therefore reach erroneous conclusions. This highlights the importance of careful analyses to disentangle the effects of multiple drivers of decline for species at risk.

Key-words: demography, harvest, invasive species, *Lantana camara*, life table response experiments, matrix models, mistletoe, non-timber forest products*Phyllanthus emblica*, *Phyllanthus indofischeri*

Introduction

Ticktin *et al.* (2012) analysed the population dynamics of two Indian dry forest tree species, *Phyllanthus emblica* L. and *P. indofischeri* Bennet (amla or Indian gooseberry), and showed that although harvest of their medicinal fruit can decrease long-term population growth rates (λ), the impact of harvest is much lower than that of a mistletoe *Taxillus tomentosus* (Heyne ex Roth) Tieghem and of an alien invasive shrub, *Lantana camara L.* We concluded, 'Our results suggest that heavy fruit harvest alone is not the driver of decline for amla and that management aimed only at prohibiting harvest will not halt the decline of this or other NTFP [non-timber forest products] species facing similar situations'. Prasad *et al.* (2014) questioned our approach and showed that *P. emblica* λ values increase when fruit harvest is banned. They therefore concluded that harvest has significant negative effects and that our management recommendations are inappropriate. Here, we address all of Prasad *et al.*'s points and demonstrate that their reanalysis is fundamentally flawed and that our conclusions hold firm.

Importance of modelling the 'real world'

We agree with Prasad *et al.* that ideally experiments are balanced and replicated. Unfortunately, when studying economically valuable resources, the feasibility of doing this differs greatly between study sites where local resource use is banned, and 'real-world' scenarios. The challenge is that 90% of tropical forests lie outside of protected areas (WWF 2002), and most are used and managed by people in some way. In these real-world scenarios, or coupled human–natural systems, it is often

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*Correspondence author. E-mail: ticktin@hawaii.edu impossible to have 'controls' because there tend to be no areas without harvest, and because people in need (including outsiders) will harvest from a control treatment if/when they need to. At the same time, the great need to go beyond controlled settings to develop a better understanding of how coupled human–natural systems actually work is widely recognized (Liu *et al.* 2007). An effective way to tackle the challenges this presents is to take empirical measurements and carefully construct models that can help elucidate how complex systems work (e.g. Jopp, Reuter & Breckling 2011). We constructed matrix models based on 10 years of data collected from our field plots and then used simulations to tease apart the relative effects of different drivers of decline for our two study species.

Prasad *et al.* claim that the literature cautions against using matrix models to predict the population trajectories of long-lived species. A recent analysis of long-term data from 82 populations of 20 plant species shows that while matrix models are poor at predicting future population sizes, simple models based on a few years of data are remarkably good at capturing the current dynamics of plant populations (Crone *et al.* 2013). The authors conclude that matrix models are very useful for 'common uses such as projecting population growth rates under current conditions and assessing the net consequences of management'. That was exactly our approach.

Unfortunately, Prasad *et al.* make false claims about how we built our models, stating that they are flawed due to 'substitution of missing data for key parameters'. They state, 'To derive the effects of high lantana and mistletoe abundance on population growth for the later period (2006–2009), when harvest was banned, the authors used transition matrices from the earlier period (1999–2005)'. That is false. For *P. emblica*, we built our matrices for the control and 'lantana and mistletoe' (presence of both lantana and mistletoe) populations from empirical measurements in those plots under those conditions (Table 1, Fig. S1, Supporting Information); that is, the effects of high abundance of lantana and mistletoe on population growth for 2006–2009 were derived from plots with high mistletoe and lantana during that time period. To tease apart the individual effects of mistletoe and lantana, we simulated populations with 'lantana only' and 'mistletoe only'. Similarly, for *P. indofischeri*, we built control and 'mistletoe' matrices from empirical measurements in those plots under those conditions. We simulated the effects of 'lantana only', and 'mistletoe and lantana' (Table 1). We show here that whether we include those simulations or not, our conclusions hold firm.

'Before vs. after' analyses confound the effects of fruit harvest and time

Fruit harvest was banned in 2006 at our study site, the Biligiri Rangaswamy Tiger Reserve (BRT). Therefore, all of our populations were harvested prior to that date and none were harvested after it. For the reasons above, it was impossible for us to have non-harvested populations prior to the ban. To evaluate the effects of fruit harvest then, we can either simulate harvest, as we did, or use a 'before' vs. 'after' analysis, as Prasad *et al.* did.

A major problem with a 'before vs. after' analysis is that the effects of the ban on fruit harvest are confounded with any other factors (climatic, biotic) that may vary over time. Prasad *et al.* reanalysed our data to show that after the ban, *P. emblica* stochastic long-term population growth rates (λs) increase across all treatments. This is correct. However, they assume that this increase is a result of the ban and use this as their main criticism of our paper. Unfortunately, they did not test that assumption.

Life table response experiments (LTREs) are a widely used method to identify which life-history transitions are most responsible for observed differences in λ values among treatments (Caswell 2001). If cessation of fruit harvest were responsible for the higher λ observed post 2006, LTREs would show that higher fecundity (number of seeds and seedlings produced per adult) would be the major contributor. However, LTRE (see Appendix S1 in Supporting Information) results show instead that the higher λ values after the ban are due almost exclusively to

Table 1. Number of *Phyllanthus emblica* and *P. indofischeri* plots under different treatments. Matrices were built directly from field data observed in the plots under those conditions

	*P. emblica**		*P. indofischeri**	
Treatment	Control	Mistletoe & Lantana	Control	Mistletoe
Year	Plots 1–3	Plots 4–6	Plots 1–6	7–10
1999–2002	No lantana or mistletoe	No lantana or mistletoe	No lantana or mistletoe	No lantana or mistletoe
2002–2005	No lantana or mistletoe	Moderate lantana & mistletoe	No lantana or mistletoe	No lantana or mistletoe
2005–2009†	No lantana or mistletoe	High lantana & mistletoe	No lantana or mistletoe	Moderate mistletoe

*We also simulated two *P. emblica* treatments: 'lantana alone' and 'mistletoe alone'. Plot # 7 had high lantana and no mistletoe and was incorporated into the simulated 'lantana' treatment. By 2008, lantana invaded *P. indofischeri* habitat but not yet our study plots. We therefore also simulated two *P. indofischeri* treatments, 'lantana' and 'mistletoe and lantana'. See Ticktin *et al.* (2012) for details on simulations.

†Fruit harvest was banned across all plots from 2006 to 2009.

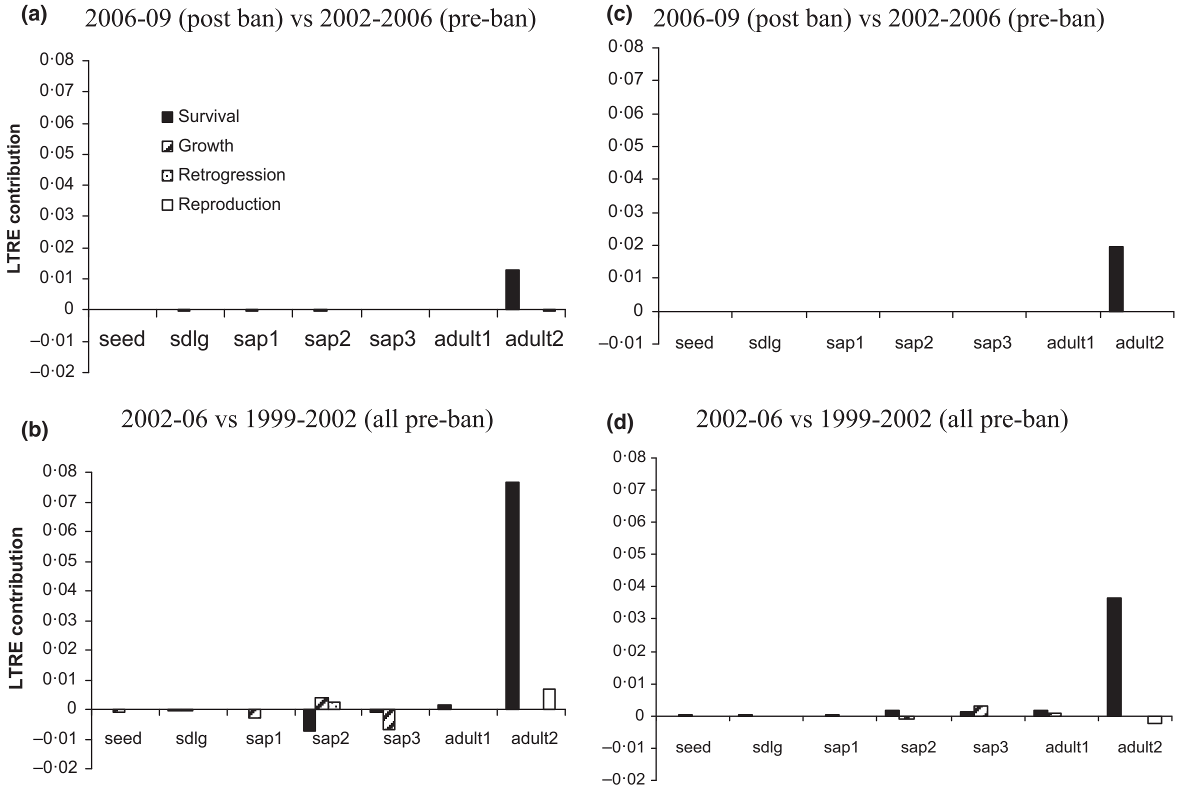

Fig. 1. Life table response experiments for *Phyllanthus emblica* control (a,b) and 'mistletoe and lantana' (c,d) populations. Analyses are based on mean matrices for the time periods indicated. Positive values represent contributions to higher long-term population growth rates observed in the time period listed first in each comparison. Legend: sdlg = seedling, sap1 = sapling1, sap2 = sapling2, sap3 = sapling3.

higher rates of adult survival (Fig. 1). Since there was no lopping of *P. emblica* trees (or branches for that matter) in our plots, this is unrelated to fruit harvest.

In fact, λ in the *P. emblica* control plots began increasing as of 2000, well before the ban (see fig. 2a in Ticktin *et al.* 2012 and Fig. S2, Supporting Information). Moreover, the difference in λs between the periods 1999–2002 and 2002–2006 – all prior to the fruit harvest ban – is six times greater than the difference in λs before vs. after the ban (2002–2006 vs 2006–2009). LTREs show that the difference is due also entirely to higher adult survival (Fig. 1b). The reasons for the increase in survival of *P. emblica* adult trees from 1999 to 2004 are not clear, but we suggest potential causes for this in Ticktin *et al.* (2012), clarifying also that these trends were consistent in other plots across the BRT.

Importantly, even though there was no fruit harvest from 2006 to 2009, λs <1 in *P. emblica* control plots (illustrated clearly in Ticktin *et al.* 2012; fig. 2, Fig. S2, Supporting Information and Prasad *et al.* 2014; fig. 1). This shows that if current conditions were to persist (e.g. no fruit harvest), populations would continue to decline. Thus, regardless of how one looks at the data, it is clear that our conclusion from Ticktin *et al.* (2012) holds: banning fruit harvest alone simply will not save amla populations.

Prasad *et al.* chose not reanalyse our *P. indofischeri* data because 'field parameters were not measured for most treatments'. Actually, the number of treatments built from empirical data was the same for *P. indofischeri* as *P. emblica* (Table 1). If Prasad *et al.* had presented those results, one would see that they do not show the same trend as *P. emblica* (Fig. 2). Although *P. indofischeri* populations were more heavily harvested than those of *P. emblica* (Ticktin *et al.* 2012 and Fig. S3, Supporting Information), there is no significant difference in λs of control populations between the 1999–2002 (pre-ban) and 2006–2009 (post-ban) periods. In addition, λs values are significantly >1, indicating increasing populations, both with and without fruit harvest. However, during 2002–2006, λs is significantly <1. As we state in Ticktin *et al.* (2012), a drought from 2002 to 2004 is probably the major contributor to the low λs during this period. This is consistent with our LTREs (Ticktin *et al.* 2012; fig. 6e,f and Fig. S4, Supporting Information) which show that lower survival and growth across most stage classes were the major contributors to the lower λ. The effects of drought were likely exacerbated in 2004–2005, when non-Soliga villagers from outside the BRT illegally cut down small trees (the only time this occurred), also discussed in Ticktin *et al.* (2012). This example further highlights the problems that

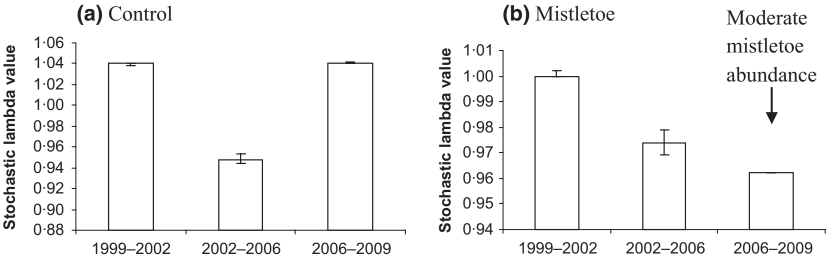

Fig. 2. Stochastic population growth rates (λs) for *Phyllanthus indofischeri* control (a) and mistletoe (b) populations. Error bars represent 95% confidence intervals. Fruit harvest was banned from 2006 to 2009.

can arise when confounding the effects of treatment with time as Prasad *et al.* did.

Why estimating fruit harvest through simulation is robust

We estimated the effects of fruit harvest by choosing one time period (2006–2009, when there was no harvest) and simulating the effects of fruit harvest. Simulating fruit removal is a widely accepted approach to assessing the effects of frugivory and fruit harvest (e.g. Dangremond, Pardini & Knight 2010; see review by Ticktin 2004) and has been shown to be consistent with empirical observations (Peres *et al.* 2003). When branch cutting or lopping is not involved, as is the case here, removing fruit from the system decreases fecundity (number of seeds and seedlings produced per adult). This is what we simulated. Secondary effects could potentially include changes in germination and survival of seeds, and in growth and survival of seedlings. This could be a result of changes in seed and seedling densities resulting from changes in patterns of frugivory, granivory and dispersal, as well as from selective harvest (smaller fruits may have lower germination and survival). In a matrix model, all those potential changes are confined to a small number of transitions: seeds and seedlings produced per adult; seed and seedling stasis and growth.

Elasticity analyses project how λ would change in response to changes in population vital rates. A small change in a vital rate with a high elasticity value will have a big impact on λ; a change in a vital rate with low elasticity will lead to very small changes in λ. Although we do not know exactly how much these transitions are reduced by harvest, elasticity analyses of *P. emblica* control and 'lantana and mistletoe' populations (including harvest and non-harvest years) reveal that changes in those matrix elements will have very little impact on λ values. Elasticity values range from 0 to 1 and for *P. emblica,* elasticities of seeds, seedlings and fecundity were all ≤0·01, while mean elasticity of adult survival was 0·81 ± 0·03 SE (Table S1, Supporting Information). Even if we consider a 'worst case' scenario and assume fruit harvest also has secondary effects by simulating large decreases in seed and seedling stasis and growth, we still find no significant differences in λ and in λs (Table S2, Supporting Information). Similarly, *P. indofischeri* fecundity elasticities were ≤0·01, mean seed and seedling elasticities were 0·02 ± 0·007 SE and 0·01 ± 0·005 SE, respectively, while mean elasticity of adult survival was 0·680 ± 0·03 SE (Table S1, Supporting Information). Low elasticity values for fecundity are consistent with tree demography studies across the globe (Franco & Silvertown 2004). Thus, we maintain that our simulations of fruit harvest are robust.

Although Prasad *et al.* claim that we fail to discuss the results of previous studies, in fact only one study (Sinha & Brault 2005) assessed the effects of fruit harvest on amla population dynamics and their findings were similar to ours. That research showed that high-intensity fire had large negative effects on *P. emblica* λs and that simulated fruit harvest increased those negative effects. However, the effect of fruit harvest was much less than that of high-intensity fire.

Prasad *et al.* claim that we exclude the possibility of other environmental factors affecting *P. emblica* populations, including fire and drought. That is false. In fact, we state clearly, 'High-intensity fire may also decrease amla population growth (Sinha & Brault 2005). This did not occur in our study plots, but may play a role elsewhere or within these plots in other years.' We also refer specifically to drought to explain the low λ values in *P. indofischeri* populations during the drought years. *P. emblica* λ values increased over the drought period.

Estimating frugivory

As Prasad *et al.* point out, frugivory varies greatly over space and time; therefore, it should not be surprising that we chose to parameterize our model with data that we collected from our field site and over the time frame of our study, instead of substituting data collected elsewhere. Our sample sizes for germination, seed predation and frugivory and matrix parameterization are sound (Table S3, Supporting Information).

Our monitoring showed that the range of *P. emblica* fruit removal was 20·3–54·8% over three seasons, and 11·3–32·6% for *P. indofischeri* over two seasons. As our experiments took place after the fruit harvest ban, frugivory rates were not limited by harvest, as Prasad *et al.* suggest. Prasad and Sukumar (2010) found higher rates of frugivory in Mudumalai, but ungulate densities are also higher there than BRT (Kumara *et al.* 2012). Prasad *et al.* refer to *P.emblica* fruit harvest rates of 90%, but this is not true. Over our study period (pre-ban), the annual proportion of *P. emblica* fruit harvested at the population level ranged from 0 to a maximum of 65% (mean = 45·2% ± 9·6 SE).

The germination rates we obtained in the greenhouse were similar to those mentioned by Prasad *et al.*, but germination in our field experiments was much lower (Table S3, Supporting Information). It is the latter, not the former, that are needed to correctly parameterize population models, and no other published studies have measured them. In addition, our seed predation experiments showed very high post-dispersal predation (Table S3, Supporting Information), which helps explain why seed germination rates in the field are so much lower than those in the greenhouse. In two germination trials with regurgitated seeds collected from the field ($N = 40$ each time), we obtained zero germination, both in the soil and on filter paper, even though non-regurgitated seeds germinated in the same media in the same experiment. Therefore, we excluded germination of regurgitated seeds from our model. When we plug our field values into our models, they produce results consistent with the number of new seedlings observed in the field. As stated in Ticktin *et al.* (2012), ungulate regurgitation of seeds likely plays an important role in dispersal but contributes little to the dynamics of the populations. While more detailed information on variation in frugivory over time would be valuable, the very low elasticity values for fecundity (Table S1, Supporting Information) indicate clearly that the effects of variation in frugivory, germination and seed predation on long-term population growth rates would be very small.

Sound recommendations for management

BRANCH CUTTING REDUCES MISTLETOE INFECTION BUT DOES NOT ERADICATE IT

While there is debate on what is considered invasive, it is well recognized that native species can become invasive due to changes in land use (Simberloff 2011). BRT has undergone enormous changes in land management since the 1970s, since the traditional Soliga practices of shifting agriculture and low-intensity (litter) fires were banned, as roads, logging and a bamboo die-off opened up areas, and with the vast expansion of lantana. Prasad *et al.* mention the importance of addressing the root cause of mistletoe expansion, which is ideal, but unrealistic over the short term since it is likely at least partially a consequence of the change in Soliga forest management practices.

Although Prasad *et al.* state that no previous researchers have labelled the mistletoe as invasive, this is incorrect (see Rist *et al.* 2010). And contrary to Prasad *et al.*'s claims, our management recommendations are not based on 'assumptions about invasiveness': whether we call the mistletoe invasive or not does not change our findings that its increase in abundance represents the primary cause of *P. emblica* adult mortality and population decline and that its effect is much larger than that of fruit harvest (Ticktin *et al.* 2012; fig. 3 and Prasad *et al.* 2014; fig. 1).

Prasad *et al.* point out that the mistletoe likely supports important mutualisms. We agree and our suggestions for management would by no means eradicate it. First, although *Phyllanthus* are the main hosts, the mistletoe also has 12 other host trees species (Rist *et al.* 2008). Second and most importantly, branch cutting only limits mistletoe expansion temporarily, but does not eradicate it. Rist *et al.* (2008) demonstrate that after branch cutting, coppicing is rapid, and that mistletoe seeds are found on coppiced branches <1 year old. They estimate that cutting provides approximately only a 3-year window without heavy mistletoe.

Mistletoes significantly decrease the quantity and quality of amla fruit production (Sinha & Bawa 2002; Setty Siddappa 2004; Ticktin *et al.* 2012). In contradiction to Prasad *et al.*'s claims, in depth studies have shown that quick coppicing and rapid recovery of fruit production occurs after branch cutting, with no increases in amla mortality (Setty Siddappa 2004; Rist *et al.* 2008).

REGENERATION IS NECESSARY FOR FUTURE FOOD SUPPLY FOR HERBIVORES

As Prasad *et al.* point out and as our data indicate, wild ungulates are the primary dispersers of amla. Our camera traps showed that 80% of amla frugivory was due to wild ungulates. It would be foolhardy to recommend management that was detrimental to them. In Ticktin *et al.* (2012), we state, 'Effective management regimes need to include a combination of lantana removal, granting permission to the Soliga to harvest lantana for furniture production, as has been done elsewhere (Bawa, Joseph & Setty 2007), and building small, temporary exclosures to exclude ungulate herbivores, in a selection of areas with and without lantana'. By 'small temporary exclosures', we refer to small (1 × 1 or 2 × 2 m) plots that protect a portion of the saplings in *P. emblica* stands and allow some to regenerate. By temporary, we refer to exclosures that can be removed in a few years once the saplings are big enough, and whose effectiveness can be monitored experimentally.

Prasad *et al.* question why we do not suggest that domestic grazing be controlled. That is because there was no grazing of domestic animals in our *P.emblica* plots and very little in general in BRT's dry deciduous forests. The grazing is by wild ungulates. There was grazing of domestic animals in the *P. indofischeri* plots. Those populations do not currently have a regeneration bottleneck but should lantana increase, limitation of domestic grazing should certainly be a priority for management.

The bottleneck we found in the regeneration of seedlings to saplings in *P. emblica* is not unique to this species, but widespread across many other species in BRT's dry forest as a result of lantana expansion (Sundaram &

Hiremath 2012). And as we mention in Ticktin *et al.* (2012), lantana removal research in a nearby protected area also clearly supports the idea that lantana expansion has limited the food supply for herbivores and led to overgrazing in lantana-free areas (Prasad 2010). If we want the BRT's wild ungulates to survive, we need to ensure that they have enough food; and they clearly will not have enough food in future if the species they eat cannot regenerate.

TARGETING HARVEST VS. OTHER DRIVERS OF DECLINE

Our paper focused on assessing the comparative effects of fruit harvest, mistletoe and lantana on amla population dynamics. Although Prasad *et al.* claim that we 'argue that harvesting is sustainable', we do not use the word 'sustainable' in our paper, or make any claims about the overall sustainability of amla harvest or the effects of fruit harvest on frugivore populations. Neither our data nor any studies to date can shed any light on that, as it would involve modelling ungulate dynamics and a much greater understanding of the role of amla in their diet. Ticktin (2004) identified assessments of the effects of fruit harvest on frugivores as a research priority nearly 10 years ago, but there has been little advance. Research on this topic would be highly valuable for informing management and was one of the reasons we initiated studies on frugivory.

To develop an objective understanding of the drivers of species decline, rigorous research and careful analyses are necessary. Our research demonstrates clearly that fruit harvest is not the lead cause of amla decline: harvest can decrease long-term population growth rates, but its effects are much lower than that of mistletoe and lantana. To conserve amla or any species effectively, we need to target the biggest drivers of decline. Banning amla fruit harvest alone simply cannot and clearly currently is not saving this species. And the pending population collapse of amla in BRT will surely have greater effects on other trophic levels than does fruit harvest.

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Supporting Information

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

Appendix S1. Life cycle diagrams, life table response experiments, elasticity analyses, and life-history parameterization for *Phyllanthus emblica* and *P. indofischeri* populations.

Fig. S1. Life cycle diagrams for amla.

Fig. S2. Projected long-term population growth rates λ (jittered) for *Phyllanthus emblica* and *P. indofischeri* populations subject to high versus low/no levels of the invasive mistletoe, *Taxillus tomentosus* and the invasive understorey shrub, *Lantana camara,* from 1999-2009.

Fig. S3. Fruit crop and proportion of amla fruit harvested per year for a) *Phyllanthus emblica* and b) *P. indofischeri* in BRT, before the harvest ban.

Fig. S4. Results of Life Table Response Experiment for *P. indofischeri* control populations (no harvest, no/low mistletoe *Taxillus tomentosus* and no/low *Lantana camara*) for a) 2003-04 versus the 1999-2009 mean matrix and b) 2004-05 versus the 1999-2009 mean matrix.

Table S1. Annual elasticity values for *Phyllanthus emblica* and *P. indofischeri* matrices.

Table S2. Stochastic long-term population growth rates (λs) and 95% confidence intervals (CI) for *Phyllanthus emblica* 'control' populations, from 2006-2009, calculated using empirical data from plots and for different fruit harvest scenarios.

Table S3. Life-history parameters, study periods and minimum and maximum sample sizes used to build matrix models for amla.