FORUM

The tangled causes of population decline in two harvested plant species: a comment on Ticktin et al. (2012)

Soumya Prasad1,2,3*, Meghna Krishnadas4, Kim R. McConkey3,5 and Aparajita Datta6

1TE-13, Biological Sciences Building, Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560055, India; 2Nature Science Initiative, 36 Curzon Road, Dehradun 248001, India; 3School of Natural Sciences and Engineering, National Institute of Advanced Studies, Indian Institute of Science Campus, Bangalore 560055, India; 4Department of Evolution, Ecology and Organismal Biology, Ohio State University, 318 W. 12th Avenue, Columbus, OH 43210-1293, USA; 5A.V. Rama Rao Research Foundation, 54 Sai Enclave, Hyderabad 500 007, India; and 6Nature Conservation Foundation, 3076/5, IV Cross, Gokulam Park, Mysore 570 002, India

Summary

2. We propose that an unbalanced design and substitution of missing data for key parameters render their matrix models flawed. They conclude that the main threats to recruitment were lantana and mistletoe invasion and recommend revoking the ban on amla harvest.
3. Our re-analyses of their data set, without substituting unavailable data, showed that cessation of harvests significantly increased stochastic growth rates of amla, despite high lantana and mistletoe cover.
4. Management recommendations by Ticktin et al. (2012) were based on the assumptions of invasiveness of a native mistletoe and grazing impacts of wild ungulates. However, interactions with amla are complex, and the recommendations made by them could have deleterious repercussions on native biota.
5. Synthesis and applications. Developing an objective understanding of harvest consequences by incorporating earlier findings and considering uncertainties in results is critical for maintaining livelihoods and ecological processes linked to amla populations.

Key-words: amla, harvest, invasion, lantana, mistletoe, NTFP, Phyllanthus emblica

Introduction

Harvesting of non-timber forest products (NTFP) from native ecosystems supports livelihoods of local communities in many parts of the world (Panayotou & Ashton 1992), but its ecological sustainability is often contentious (Siebert 2004). Comprehensive assessment of sustainability is challenging since it involves monitoring a suite of parameters, at genetic, population, community and landscape levels, across multiple generations, and inclusion of social, economic and political drivers (Shahabud-din & Prasad 2004; Siebert 2004). While it is not possible for a single study to integrate all these parameters, applied research must be designed to ensure adequate predictive power for assessments of sustainability. Studies examining the impacts of NTFP harvest have been critiqued for a lack of objectivity (Siebert 2004). As an applied science that informs management of natural resources, NTFP studies must be methodologically rigorous, objectively test proposed models of conservation action and be specific in extrapolating results for management (Shaanker & Ganeshaiah 2010).

The debate on ecological sustainability of forest produce harvest has been enriched by extensive research on the amla (ibid) and Brazil nut systems (Peres et al. 2003) from tropical Asia and South America, respectively. Amla species Phyllanthus emblica Linn. and P. indofischeri

*Correspondence author. E-mail: prasadsoumya@gmail.com

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Bennet (Euphorbiaceae) are medium-sized trees from tropical dry forests in south Asia. Their fruit, a rich source of vitamin C, is used in pickles, hair-oil and traditional medicine. Wild amla harvest contributes up to 11% of incomes of forest-dependent communities in India (Shankar et al. 1996). Research on the amla system has largely emerged from long-term socio-ecological monitoring at Biligiri Rangaswamy Temple Tiger Reserve (BRT), Southern India (540 km²; 11–13° N, 77–78° E; reviewed in Shaanker et al. 2004; Sinha & Brault 2005).

Ticktin et al. (2012) attempted to unravel three potential drivers of a predicted population decline in two amla species at BRT: fruit harvesting by the Soliga people, mistletoe Taxillus tomentosus Tiegh. infection and invasion by lantana Lantana camara Linn. However, Ticktin et al. failed to measure important ecological parameters influencing amla population dynamics. We question their justification for substituting life-history parameters from different species or treatment combinations to model dynamics of species or treatments with incomplete data. Further, several management recommendations that ensue are unsubstantiated, and Ticktin et al. (2012) fail to discuss findings from previous studies that differ from their conclusions (Shaanker et al. 2004; Shahabuddin & Prasad 2004; Sinha & Brault 2005; Rist, Shaanker & Ghazoul 2011).

Our concerns are addressed in three inter-related points which we describe in the following sections.

**INADEQUACIES IN DESIGN AND ANALYSES TO DISENTANGLE THE CAUSES OF AMLA POPULATION DECLINE**

**Design and treatments**

Ticktin et al. (2012) attempted to disentangle effects of fruit harvest, lantana invasion and mistletoe over-abundance on amla population dynamics. They consider two levels for mistletoe and lantana abundance (low, high) and incorporate harvest as a temporal additive effect (1999–2005 harvested; 2006–2009 harvest free). To understand simultaneous effects (Downes 2010), a balanced study design involving at least two levels for each driver would necessitate replicate plots within eight treatment combinations (Table 1). In total, Ticktin et al. had seven plots for *P. emblica* and 10 for *P. indofischeri* (monitored from 1999–2006), but do not indicate the number of plots under different treatments for each amla species. From the information provided, it appears that four out of eight treatments were not measured under field conditions for *P. emblica*, while six were not quantified for *P. indofischeri* (Table 1).

In their matrix models, Ticktin et al. (2012) substituted transition probabilities from other scenarios for treatment combinations for which field data were unavailable. For *P. indofischeri*, they used seedling and sapling transition probabilities from *P. emblica* plots with high lantana and low mistletoe cover. However, there are fundamental differences between these two species, in terms of habitat occupied, adult mortality, recruitment patterns and rarity (Ganesan & Setty 2004). Further, mistletoe and lantana abundance peaked in the study plots during a harvesting ban (after 2005–2006), and the impact of harvesting was measured only when mistletoe and lantana abundance were low. To derive the effects of high lantana and mistletoe abundance on population growth for the later period, when harvest was banned, the authors used transition matrices from the earlier period (1999–2005). Thus, Ticktin et al. (2012) do not have data sets for conditions in which fruit harvest would interact with mistletoe and lantana to address their objective of examining additive effects of harvests and invasions on amla demographics. Matrix population models are useful tools to assess multiple stressors influencing plant population dynamics. However, as cautioned by Bieyszchudek (1999), projections from matrix models may be misleading, if samples sizes are inadequate to provide transition probabilities and data sets span too few years to accurately capture interannual environmental variability.

**Life-history parameters**

Ticktin et al. (2012) monitored plots for 10 years, yet most life-history parameters for each treatment were measured for one to three years (please see Appendix S1 in Supporting Information). Ticktin et al. (2012) state that ‘As mistletoe only affects vital rates of adults, to build

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Low mistletoe, Low lantana (Control)</th>
<th>High mistletoe, Low lantana (Mistletoe)</th>
<th>Low mistletoe, High lantana (Lantana)</th>
<th>High mistletoe, High lantana (Mistletoe· Lantana)</th>
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<tbody>
<tr>
<td></td>
<td>Harvest free 2006–2009†</td>
<td>NA</td>
<td>2006–2009†</td>
<td>NA†</td>
</tr>
<tr>
<td><em>P. indofischeri</em></td>
<td>Harvested 1999–2005‡</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Harvest free 2006–2009†</td>
<td>NA</td>
<td>NA</td>
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</table>

*Unreported number of *P. emblica* plots stated to have moderate lantana in harvested period (2002–2005).
†Sample sizes not reported.
‡Unreported number of *P. emblica* plots stated to have high lantana and moderate mistletoe levels in harvest-free period (2006–2009).
mistletoe treatment matrices, we used the transitions of adults from plots with high densities of mistletoes and transitions of the smaller sizes from plots with no or low lantana. Because lantana only affects seeds, seedlings and saplings, for the lantana treatment, we did the reverse. This indicates that the transition probabilities may not reflect the true parameter values for plots under mistletoe and lantana treatments and are based on untested assumptions. Instead of substituting parameters, the transitions as recorded in the plots under each treatment would have provided more reliable estimates.

Ticktin et al. (2012)’s experiments on fruit removal, seed survival in seed banks and seed germination are reported incompletely in their manuscript and supporting information. They state that they found no variation between treatments for proportion of fruit removed by frugivores and seed survival within seed banks. However, results from *P. emblica* populations in similar habitat show high levels of spatio-temporal variation in frugivory rates both within seasons and across years (Prasad & Sukumar 2010), and also between harvested and harvest-free scenarios (Prasad, Chellam & Krishnaswamy 2001). In harvest-free scenarios, wild ruminants consume over 80% of the amla fruit crop (Prasad & Sukumar 2010). It is surprising that harvesting rates of over 90% by people at BRT did not reduce the proportion of fruit crop removed by frugivores in the harvest treatments. Similarly, Ticktin et al. (2012) state that the germination rates for seeds regurgitated by deer were very low and rates of seed predation were high, without reporting actual percentages of germination or predation. Studies on amla populations in similar habitat report 20–30% germination of wild ruminant-regurgitated seeds (Prasad et al. 2006). The sampling adequacy of Ticktin et al. (2012)’s camera trapping effort, germination and predation trials cannot be assessed since results and sample sizes under different treatments are not provided (Appendix S1). These important contrasts with previous studies outlined above, and the potential limitations of the current study should have been discussed given the direct implications for amla population dynamics.

**DISENTANGLING IMPACTS OF SIMULTANEOUS DRIVERS ON AMLA POPULATIONS: A RE-ANALYSES**

We used matrices provided in the supporting information of Ticktin et al. (2012) and the same chronology of invasion and harvests as presented by Ticktin et al. (Appendix S2). We used only *P. emblica* for our re-analyses because field parameters were not measured for most treatments for *P. indofischeri* (Table 1). The main deviation in our approach from Ticktin et al.’s was that we avoided substituting or simulating effects of treatment combinations that were not observed under field conditions for *P. emblica* (Table 1). Ticktin et al. (2012) describe three temporal stages in their study – pre-invasion (1999–2002), moderate invasion (2002–2005) and high invasion (2006–2009). All plots in the pre-and moderate invasion periods were harvested. Therefore, matrices can only be analysed without a control for harvest. We re-analysed Ticktin et al. (2012)’s matrices for three periods of harvest and invasion history (a) Harvested, with low invasion, 1999–2002, (b) Harvested, with moderate invasion, (c) Not harvested, high invasion. We examined growth rates for the four invasion treatments: control, mistletoe (high mistletoe, low lantana), lantana (low lantana, low mistletoe cover) and mistletoe–lantana (high mistletoe and lantana) in these three periods.

For all treatments across all periods, the mean deterministic growth rate $\lambda_m$ and stochastic growth rates $\lambda_s$ (Fig. 1 a,b) were below one, indicating a declining population. The confidence intervals for $\lambda_s$ indicate non-overlapping differences in growth rates between treatments. The growth rates $\lambda_m$ and $\lambda_s$ were similar between treatments during the pre-invasion period. In all treatments, $\lambda_m$ and $\lambda_s$ increased after harvest cessation, a period with high lantana and mistletoe (Fig. 1).

In control plots that are indicative of differences between harvested and non-harvested populations without invasion, $\lambda_m$ and $\lambda_s$ showed an increase during 2002–2005 (which included harvest) with a further increase following the cessation of harvests (Fig. 1). High mistletoe cover appears to have reduced growth rates, with plots in the ‘mistletoe’ category having lower growth rates than controls. However, even ‘mistletoe’ plots with high cover would have provided more reliable estimates.

![Fig. 1. Predicted growth rates of amla *Phyllanthus emblica*: (a) mean deterministic lambda ($\lambda_m$), and (b) stochastic lambda ($\lambda_s$) for four treatments during three periods of invasion and harvest history derived from Ticktin et al. (2012). Error bars indicate standard error.](image-url)
show an increase in growth rates after harvest cessation. Growth rates in the ‘Lantana’ plots were similar to control plots; $\lambda_m$ and $\lambda_n$ were higher in the moderate invasion period than in the pre-invasion period and showed a further, substantial increase in the high invasion period during which harvest was banned. In the plots that had high mistletoe and lantana, although $\lambda_m$ and $\lambda_n$ were lower than control plots during the period corresponding to pre- and moderate invasion, harvest cessation increased growth rates (Appendix S2).

Interestingly, the $\lambda_{mv}$ values for the control plot (no invasion) appeared to fluctuate during the periods when harvest was occurring (Fig. 1), which is indicative of stochastic or unmeasured factors that are influencing growth rates of *P. emblica* in these plots. Nevertheless, Ticktin et al. (2012) argue that the effects of other factors, such as droughts and fires, which could influence plant population dynamics, were unlikely to have important effects during their study period. A large part of their post-harvest study period coincided with a drought in southern India (2000–2004) that resulted in increased mortality in woody plant species in an adjoining forest site (Mudumalai National Park) with a similar floral and faunal composition (Suresh, Dattaraja & Sukumar 2010). Further, an earlier study at BRT observed that fires, which are often set by harvesters, had 2–3-year return intervals and had negative impacts on production, growth and population persistence of amla species (Sinha & Brault 2005). Given these earlier findings and the fire history of this dry forest region (Kodandapani, Cochrane & Sukumar 2008), it is not evident why Ticktin et al. (2012) excluded quantifying fires as a driver of change in amla populations, especially since their main purpose was to disentangle the multiple stressors that influence amla populations.

**Unsubstantiated Management Recommendations**

**An over-simplified account of mistletoe invasion and its control**

Invasive species are native or alien organisms that have spread into new environments and often have a large impact on the new environment (Valéry et al. 2008). The mistletoe *T. tomentosus* referred to as invasive by Ticktin et al. (2012) is native to BRT; the quantitative data necessary to confirm a population spread of this mistletoe are not available, and no previous researchers have labelled it as invasive (Rist, Shaanker & Ghazoul 2011). While mistletoes have increased in abundance in some countries mainly due to changes in land-use practices (Norton & Reid 1997), range expansion is rare (Ward, Shrestha & Musli 2006) and they have rarely been classified as invasive. In fact, mistletoes may be keystone resources involved in important mutualisms with native fauna and may provide critical resources for native fauna (Davidar 1983; Norton & Reid 1997; Watson & Herring 2012). There is evidence for seed dispersal and pollination mutualisms between flowerpeckers and *Taxillus* in southern India (Davidar 1983). In Australia, removal of mistletoes induced a 21% decline in bird species richness (Watson & Herring 2012). Hence, Ticktin et al. (2012)’s recommendation for mistletoe control may have negative impacts on native fauna.

Heavy infestation by mistletoe is detrimental for host growth, fecundity and, more rarely, causes mortality in several study systems (Ward, Shrestha & Musli 2006; Norton & Reid 1997). Increases in native mistletoe abundance are associated with ecosystem disturbance (Norton & Reid 1997). BRT has experienced considerable land-use changes in recent years, including increased harvesting (Shankar et al. 1996), grazing by domestic livestock (Ganesan & Setty 2004), fire regimes (Kodandapani, Cochrane & Sukumar 2008), and increases in invasive lantana (Sundaram & Hiremath 2012). Ticktin et al. (2012) propose lopping of branches to control mistletoes in BRT, but such an approach does not address the underlying causes of increased mistletoe infection (Norton & Reid 1997) and may have strong negative impacts on amla growth rates according to the researchers who have directly assessed lopping impacts (Sinha 2000). Control of native species must be judicious, and referring to a species repeatedly as invasive, without proof of this classification, creates a biased precedent for its widespread lethal control (Shaanker & Ganeshaiah 2010).

**Importance of amla’s only known seed dispersers is not considered in management recommendations**

Ticktin et al. (2012) conclude that wild ungulate grazing is a significant cause of amla recruitment failure and hence argue for wild ungulate exclusion in some areas, although this was not specifically tested. However, wild ungulates are primary dispersers of *P. emblica* (Prasad et al. 2006), and as a tiger reserve, conservation of wild ungulates is an important management goal for BRT (Jhala et al. 2010). Ungulate grazing may result in sapling decline, but exclusion of wild ungulates is an unreasonable recommendation if, as stated by Ticktin et al. (2012), areas suitable for wild ungulate browsing are already reduced due to lantana invasion. Ganesan & Setty (2004) suggested that grazing by domestic livestock was probably a significant driver of sapling mortality at BRT. A reduction in domestic livestock may reduce overall grazing pressure while maintaining amla populations and the conservation objectives of the reserve.

Ticktin et al. (2012) argue that harvesting is sustainable because collectors target trees with large crops, which they believe will allow recruitment in intermittent years when crops are small. This is a simplistic, unverified approach to ascertaining sustainability of harvests (Shahabuddin & Prasad 2004; Siebert 2004). Research on *P. emblica* has shown that frugivores prefer trees bearing large crops or located in dense clusters of fruiting trees (Prasad &
Sukumar 2010). It may therefore be incorrect to assume that trees bearing small crop are sufficient for dispersal and recruitment without thoroughly investigating trophic-level consequences of harvest.

CONCLUSION

Ticktin et al. (2012) make urgent management recommendations for lantana and mistletoe control, but not amla fruit harvest. Our re-analyses indicates, however, that in spite of high lantana and mistletoe cover, cessation of fruit harvest significantly increases growth rates of *P. emblica* and stochastic factors may also be at play. Our conclusions are concurrent with earlier research demonstrating that harvest practices negatively impact amla populations (reviewed in Shaanker et al. 2004; Sinha & Brault 2005).

A rigorous understanding of harvest consequences is critical to developing management protocols that can maintain both livelihoods and ecological processes (Peres et al. 2003; Shaanker et al. 2004; Siebert 2004). Long-term data sets, especially those examining simultaneous effects of multiple drivers, are often incomplete and noisy. Conservation guidelines are almost always derived from incomplete data sets. However, to be more effective, guidelines should consider caveats, uncertainties in findings and be derived in combination with earlier studies. Bayesian approaches have allowed population modellers to incorporate prior information and explicitly convey uncertainty about effects of simultaneous drivers and management alternatives (Evans, Holsinger & Menges 2010). Decision-making tools that allow integrated analyses of multiple criteria are also increasingly being used for uncertainty assessment of management alternatives derived from noisy data sets (Ascough et al. 2008). As scientists inform an applied field with immediate implications in fast-declining natural habitats, we must make recommendations which integrate prior knowledge and are commensurate with the uncertainty and limitations of our study methods.

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References


Sinha, A. (2000) Sustainability of fruit extractions from two non-timber forest tree species, *Phyllanthus emblica* and *P. indicofischeri*, in the forests of south India. Dissertations. University of Massachusetts, Boston, Massachusetts, USA.


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Supporting Information

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

**Appendix S1.** Life-history parameters incorporated in Ticktin et al. (2012)’s models.

**Appendix S2.** Re-analyses of matrix population models