

FORUM

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

Soumya Prasad^{1,2,3*}, Meghna Krishnadas⁴, Kim R. McConkey^{3,5} 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

1. Ticktin *et al.* (2012) attempted to disentangle multiple stressors impacting harvested populations of amla (*Phyllanthus emblica* and *P. indofischeri*) [Ticktin *et al.* (2012) Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. *Journal of Applied Ecology*, **49**, 774–784.].
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 (Shahabuddin & 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 & Ganeshiah 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

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 Biezychudek (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 1. Treatment combinations required for a balanced study design. Number of plots reported under each treatment by Ticktin *et al.* (2012) are presented within parentheses. NA refers to treatments not observed by Ticktin *et al.* (2012)

	Treatments	Low mistletoe, Low lantana (Control)	High mistletoe, Low lantana (Mistletoe)	Low mistletoe, High lantana (Lantana)	High mistletoe, High lantana (Mistletoe- Lantana)
<i>P. emblica</i>	Harvested	1999–2002 (7) 2002–2005 (3)	NA	NA*	2002–2005 (4)
	Harvest free	2006–2009 [†]	NA	2006–2009 [†]	NA [‡]
<i>P. indofischeri</i>	Harvested	1999–2005 [†]	NA	NA	NA
	Harvest free	2006–2009 [†]	NA	NA	NA

*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 har-

vested. 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 (high 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 λ_m and stochastic growth rates λ_s (Fig. 1 a,b) were below one, indicating a declining population. The confidence intervals for λ_s indicate non-overlapping differences in growth rates between treatments. The growth rates λ_m and λ_s were similar between treatments during the pre-invasion period. In all treatments, λ_m and λ_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, λ_m and λ_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

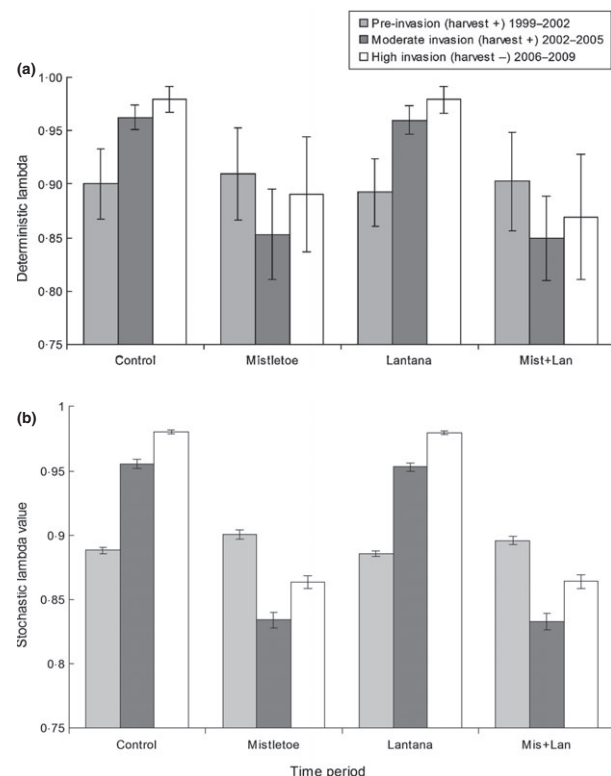


Fig. 1. Predicted growth rates of amla *Phyllanthus emblica*: (a) mean deterministic lambda (λ_m), and (b) stochastic lambda (λ_s) for four treatments during three periods of invasion and harvest history derived from Ticktin *et al.* (2012). Error bars indicate standard error.

show an increase in growth rates after harvest cessation. Growth rates in the 'Lantana' plots were similar to control plots; λ_m and λ_s 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 λ_m and λ_s were lower than control plots during the period corresponding to pre- and moderate invasion, harvest cessation increased growth rates (Appendix S2).

Interestingly, the λ_m 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 & Ganeshiah 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 informing 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.

Acknowledgements

We thank Karpagam Chelliah, Geetha Ramaswami, David Watson, Sachin Sridhara, Priya Davidar and an anonymous reviewer for inputs.

References

- Ascough, J.C., Maier, H.R., Ravalico, J.K. & Strudley, M.W. (2008) Future research challenges for incorporation of uncertainty in environmental and ecological decision-making. *Ecological Modelling*, **219**, 383–399.
- Biezychudek, P. (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications*, **9**, 1278–1287.
- Davidar, P. (1983) Similarity between flowers and fruits in some flower-pecker pollinated mistletoes. *Biotropica*, **15**, 32–37.
- Downes, B.J. (2010) Back to the future: little-used tools and principles of scientific inference can help disentangle effects of multiple stressors on freshwater ecosystems. *Freshwater Biology*, **55**, 60–79.

- Evans, M.E.K., Holsinger, K.E. & Menges, E.S. (2010) Fire, vital rates, and population viability: a hierarchical Bayesian analysis of the endangered Florida scrub mint. *Ecological Monographs*, **80**, 627–649.
- Ganesan, R. & Setty, R.S. (2004) Regeneration of amla, an important non-timber forest product from southern India. *Conservation and Society*, **2**, 365–375.
- Jhala, Y.V., Qureshi, Q., Gopal, R. & Sinha, P.R. (Eds.) (2010) *Status of the Tigers, Co-Predators, and Prey in India, 2010*. National Tiger Conservation Authority, Govt. of India, New Delhi and Wildlife Institute of India, Dehradun. TR 2011/003/pp 302.
- Kodandapani, N., Cochrane, M.A. & Sukumar, R. (2008) A comparative analysis of spatial, temporal, and ecological characteristics of forest fires in seasonally dry tropical ecosystems in the Western Ghats, India. *Forest Ecology and Management*, **256**, 607–617.
- Norton, D.A. & Reid, N. (1997) Lessons in ecosystem management from management of threatened and pest Loranthaceous mistletoes in New Zealand and Australia. *Conservation Biology*, **11**, 759–769.
- Panayotou, T. & Ashton, P.S. (1992) *Not by Timber alone – Economics and Ecology for Sustaining Tropical Forests*. Island Press, Washington, USA.
- Peres, C.A., Baider, C., Zuidema, P.A., Wadt, L.H.O., Kainer, K.A., Gomes-Silva, D.A.P. *et al.* (2003) Demographic threats to the sustainability of Brazil nut exploitation. *Science*, **302**, 2112–2114.
- Prasad, S., Chellam, R. & Krishnaswamy, J. (2001) Fruit removal patterns and dispersal of *Emblia officinalis* (Euphorbiaceae) at Rajaji National Park, India. In: *Tropical Ecosystems: Structure, Diversity & Human Welfare*, (eds K.N. Ganeshaiah, R.U. Shaanker & K.S. Bawa.), pp 513–516. Oxford & IBH Co. Pvt. Ltd, New Delhi.
- Prasad, S. & Sukumar, R. (2010) Context-dependency of a complex fruit-frugivore mutualism: temporal variation in crop size and neighbourhood effects. *Oikos*, **119**, 514–523.
- Prasad, S., Krishnaswamy, J., Chellam, R. & Goyal, S.P. (2006) Ruminant-mediated seed dispersal of an economically valuable tree in Indian dry forests. *Biotropica*, **38**, 679–682.
- Rist, L., Shaanker, R.U. & Ghazoul, J. (2011) The spatial distribution of mistletoe in a southern Indian tropical forest at multiple scales. *Biotropica*, **43**, 50–57.
- Shaanker, R.U. & Ganeshaiah, K.N. (2010) Is there enough science for conservation action? *Biotropica*, **42**, 463–565.
- Shaanker, R.U., Ganeshaiah, K.N., Krishnan, S., Ramya, R., Meera, C., Aravind, N.A. *et al.* (2004) Livelihood gains and ecological costs of non-timber forest product dependence: assessing the roles of dependence, ecological knowledge and market structure in three contrasting human and ecological settings in south India. *Environmental Conservation*, **31**, 242–253.
- Shahabuddin, G.S. & Prasad, S. (2004) Assessing ecological sustainability of Non-Timber Forest Produce extraction: the Indian scenario. *Conservation and Society*, **2**, 236–250.
- Shankar, U., Murali, K.S., Shaanker, R.U., Ganeshaiah, K.N. & Bawa, K.S. (1996) Extraction of non-timber forest products in the forests of the Biligiri Rangan Hills, India. 3. Productivity, extraction and prospects of sustainable harvest of amla *Phyllanthus emblica* (Euphorbiaceae). *Economic Botany*, **50**, 270–279.
- Siebert, S.F. (2004) Demographic effects of collecting rattan cane and their implications for sustainable harvesting. *Conservation Biology*, **18**, 424–431.
- Sinha, A. (2000) *Sustainability of fruit extractions from two non-timber forest product tree species, Phyllanthus emblica and P. indofischeri, in the forests of south India*. Dissertation. University of Massachusetts, Boston, Massachusetts, USA.
- Sinha, A. & Brault, S. (2005) Assessing sustainability of non-timber forest product extractions: how fire affects sustainability. *Biodiversity and Conservation*, **14**, 3537–3563.
- Sundaram, B. & Hiremath, A.J. (2012) *Lantana camara* invasion in a heterogeneous landscape: patterns of spread and correlation with changes in native vegetation. *Biological Invasions*, **14**, 1127–1141.
- Suresh, H.S., Dattaraja, H.S. & Sukumar, R. (2010) Relationship between annual rainfall and tree mortality in a tropical dry forest: results of a 19-year study at Mudumalai, southern India. *Forest Ecology and Management*, **259**, 762–769.
- Ticktin, T., Ganesan, R., Paramesha, M. & Setty, S. (2012) Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. *Journal of Applied Ecology*, **49**, 774–784.

- Valéry, L., Fritz, H., Lefeuvre, J. & Simberloff, D. (2008) In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions*, **10**, 1345–1351.
- Ward, D., Shrestha, M.K. & Musli, I. (2006) Are invasive mistletoes killing *Ziziphus spina-christi*? *Israel Journal of Plant Sciences*, **54**, 113–117.
- Watson, D.M. & Herring, M. (2012) Mistletoe as a keystone resource: an experimental test. *Proceedings of the Royal Society B*, **279**, 3853–3860.

Received 19 April 2013; accepted 29 August 2013
Handling Editor: Philip Hulme

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