Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees

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Summary

1. Tropical plant populations are often subject to multiple types of anthropogenic disturbance. Effective management requires disentangling the effects of these disturbances and prioritizing interventions for the driver(s) most responsible for population decline. However, the effects of multiple drivers on plant population dynamics are rarely examined.

2. We assessed the independent and combined effects of common anthropogenic disturbances on the transient and long-term population dynamics of two economically important, declining tree species in an Indian dry forest. Specifically, we drew on 10 years of demographic monitoring to assess the effects of non-timber forest product (NTFP) harvest and two invasive species (an understorey shrub *Lantana camara* and a mistletoe *Taxillus tomentosus*) on amla (*Phyllanthus emblica* and *Phyllanthus indofischeri*) populations.

3. Although fruit harvest has been blamed for declining amla populations, the current policy and management strategies implemented to restrict it have little effect on long-term stochastic growth rates (λ_s) of amla both with and without invasive species. In contrast, mistletoes significantly decreased λ_s of both species.

4. Lantana had both direct and indirect effects on *P. emblica,* causing a regeneration bottleneck. Lantana had a direct negative effect on seeding and sapling growth, whereas populations without lantana experienced higher levels of grazing by wild animals. Over 10 years, *P. emblica* populations dropped to 16% of their original size in areas with invasive species.

5. *Synthesis and applications.* Our results illustrate that mistletoe and lantana, not fruit harvest, are the main drivers of amla decline, and these species are likely to be driving the decline of other Indian dry forest tree species. Management directed only at limiting fruit harvest will be ineffective. Instead, control of both invasive species combined with temporary protection from grazing is urgently needed. The ban on fruit harvest in Indian protected areas is not an effective conservation policy for these species. Harvest is not necessarily the main cause of decline for NTFP species. Management plans for NTFP and other at-risk species must consider the relative effects of different drivers of decline, including direct and indirect effects of invasive species.

Key-words: demography, fruit harvest, India, invasive species, *Lantana camara*, matrix models, mistletoe, non-timber forest products, *Phyllanthus emblica*, *Phyllanthus indofischeri*

Introduction

Plant populations are often subject to multiple sources of anthropogenic disturbance. This is especially true in the tropics, where 90% of forests lie outside of protected areas (WWF 2002) and where many protected areas are also used to some extent by the millions of forest-dependent peoples who live in and around them. Harvest of timber and non-timber forest products (NTFP), invasive species spread, grazing by

domestic animals and anthropogenic fire are routine and concurrent disturbances experienced by plant populations in tropical forests (IUCN 2010). Although many studies have identified the effects of specific types of anthropogenic disturbance on plant population dynamics, the effects of multiple concurrent sources of disturbance have rarely been examined (Crone *et al.* 2011; but see Martinez-Ramos, Anten & Ackerly 2009). This is problematic because effective management for conservation requires disentangling the effects of different drivers to identify those most responsible for species decline. As limited resources require managers to prioritize interventions,

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it is critical that they target the most important drivers of decline for at-risk populations. These targets may not be obvious when there are several potential drivers. Moreover, because interactions among ecological processes are often non-additive (Didham *et al.* 2007), it can be difficult to accurately predict the effects of more than one type of disturbance. In addition, indirect effects of disturbance can be hard to detect. For example, invasive species can affect co-occurring species through direct effects such as recruitment limitation, but also indirectly through processes such as apparent competition (Dangremond, Pardini & Knight 2010). Finally, disentangling the effects of multiple disturbance factors is difficult with short-term data sets, but longer-term studies are still rare, especially in the tropics (Crone *et al.* 2011).

In this study, we draw on a 10-year demographic data set to disentangle the effects of common forms of anthropogenic disturbance on the decline of two economically important tropical dry forest trees in India. Specifically, we assess the independent and combined effects of NTFP harvest and two invasive species on the population dynamics of *Phyllanthus emblica* L. and *Phyllanthus indofischeri* Bennet Euphorbiaceae. Amla fruits are heavily harvested from dry forests across the Indian subcontinent. They are key components in Indian herbal medicines, food, cosmetics and other products, and sales can make very important contributions to local livelihoods, especially in indigenous communities (Sandemose 2009). Amla are among hundreds of tropical tree species harvested for their fruit. While wild fruit harvest is often sustainable (Ticktin 2004), heavy long-term harvest of some species can lead to decline (Peres *et al.* 2003).

Dry forests across India have been invaded by lantana *Lantana camara* L., Verbenaceae, a neotropical understorey shrub, which is highly invasive across parts of South Asia, Australia, Africa and the Pacific Islands (Sundaram 2011). Dense lantana stands can alter the richness and composition of understorey plant communities and stall regeneration of native species beneath them (e.g. Gooden *et al.* 2009; Sundaram 2011).

Amla populations are also affected by mistletoe *Taxillus tomentosus* Heyne ex Roth Tieghem, Loranthaecae, which infects the canopies of adult amla trees (> 5 cm d.b.h.), as well as 14 other species (Rist *et al.* 2008). As with mistletoes in Australia, New Zealand and elsewhere (e.g. Norton & Reid 1997), this native hemiparasite has likely become invasive as a result of changes in land management that increase edge habitat (Rist *et al.* 2008). Mistletoes can decrease survival and reproduction of host trees (Reid, Stafford Smith & Venables 1992; Sinha & Bawa 2002; Setty Siddappa 2004), but how they alter the long-term population growth rates of their hosts has not been assessed.

In protected areas across India, the harvest of amla and other NTFP is highly contentious. Harvesters and forest managers have perceived a clear decline in amla populations, but forest managers attribute it to overharvest of fruit, while harvesters blame mistletoe (Rist *et al.* 2010). In 2004, the Indian government banned the harvest of all NTFP, including amla, from protected areas. The ban was an attempt to improve con-servation but was not based on ecological studies. It had serious negative consequences for the livelihoods of indigenous harvesters (Sandemose 2009).

Effective conservation and management of amla, and the many other plant species subject to multiple anthropogenic disturbances, requires clear identification of the drivers of decline. We addressed the following questions: (i) What are the single and combined effects of fruit harvest, lantana and mistletoe invasion on long-term and transient population growth rates of *P. emblica* and *P. indofischeri*? (ii) Are the effects of fruit harvest and invasive species additive? (iii) Do the effects of fruit harvest and invasive species differ between *P. emblica* and *P. indofischeri* populations? (iv) Given 1–3, what are the best strategies for conserving these species?

We hypothesized that fruit harvest has little effect on amla populations, because reduction in fecundity tends to have little effect on population growth rates of woody species (Franco & Silvertown 2004; Ticktin 2004). We expected both mistletoe and lantana to decrease amla population growth rates, but expected a greater effect of mistletoe because long-lived woody species tend to be most sensitive to changes in adult survival (Franco & Silvertown 2004). We also predicted that fruit harvest would have a negative effect on amla populations in the context of invasive species. Finally, we expected that *P. indofischeri* may be less tolerant of invasive species because its habitat is often subject to additional anthropogenic disturbances such as firewood harvest and grazing by livestock, and therefore, it may have higher rates of mortality than *P. emblica*.

Materials and methods

STUDY SITE AND SPECIES

This study took place in the Biligiri Rangaswamy Temple Wildlife Sanctuary (BRT; 11–13′ N, 77–78′ E), located in the south Indian state of Karnataka and part of the Western Ghats Biodiversity hot-spot. BRT extends over 540 km² and supports a range of forests but this study took place in the dry deciduous forests (900–1200 m, mean annual rainfall 1362 ± 159 mm) and scrub forests (600–900 m, rainfall 898 ± 164 mm). Over the past 15–20 years, lantana has spread across the BRT forming dense understorey stands (Sundaram 2011). About 6000 indigenous *Soliga* reside in BRT, and between 10% and 85% of household income is derived from NTFP extraction (Sandemose 2009). When BRT was declared a wildlife sanctuary in 1974, *Soliga* traditional shifting agriculture and hunting practices were prohibited, and they were given usufruct rights to gather NTFP. The *Soliga* harvest amla fruits directly from the trees before they mature, by beating the branches with sticks or sometimes lopping the fruiting branches. The 2004 federal ban on NTFP harvest was implemented in BRT in 2006, and amla fruit harvest did not occur from 2006 to 2009.

Phyllanthus emblica and *P. indofischeri* are small trees, up to 10–15 m in height, respectively. *Phyllanthus emblica* is distributed throughout dry deciduous forests of South and Southeast Asia, but *P. indofischeri* is endemic to scrub forests of south India's Deccan region (Ganesan & Siddappa Setty 2004). Fruits of both species have fleshy exocarps that mature from December to February. The stony endocarp dehisces and the seeds are mechanically dispersed. Ungu-

lates eat the fleshy fruit and regurgitate the endocarps containing the seeds.

MEASURING AMLA DEMOGRAPHIC RATES

In December 1999, we established 17, 10×100 m permanent plots to monitor amla populations. Ten plots were located in scrub forest (for *P. indofischeri*) and seven plots in dry forests (for *P. emblica*). Plots were censused annually for 10 years (1999–2009), and at each census, all amla individuals were measured and new recruits were tagged. We measured basal diameter for individuals < 1·3 m high and d.b.h. for all others. Every year the number of fruit per tree was counted on a set of trees inside and outside the plots ($N = 163$ *P. emblica* and $N = 176$ *P. indofischeri*), in November, before the fruits mature. To calculate the number of fruit harvested per tree, fruit were also counted after harvest occurred. A total of 1476 *P. emblica* and 1509 *P. indofischeri* individuals were used in the analyses.

PARAMETERIZATION OF MATRIX MODELS

We used matrix models (Caswell 2001) to test the effects of fruit harvest and invasive species on amla dynamics. We classified amla individuals into seven stages based on basal area and life history: seeds in the seedbank; seedlings (< 1 year old), small saplings ≤0·072 cm², medium saplings $0·072 < \times ≤0·787$ cm², large saplings $0·787 < \times ≤19·643$ cm², small adults (reproductive in *P. indofischeri* only) $19·643 < \times ≤63·643$ cm², and large adults > 63·643 cm² (reproductive in both species). We built 7×7 Lefkovitch stage-structured transition matrices directly from the annual census field data. Amla germination, seedling survival, survival of seeds in the seedbank and the proportion of fruit removed by frugivores were estimated from field and nursery experiments in 2005–2008 and used to calculate the fecundity values in the matrices (Appendix S1, Supporting Information).

At the initiation of this study, there was very little or no lantana or mistletoe presence across all plots. By 2005, four *P. emblica* plots were highly invaded by both mistletoe and lantana, and three plots had little or none of each (Table 1). One plot was invaded by lantana only. To test the effects of invasive species on *P. emblica* demographic rates, we built separate matrices for each year and each of four treatments: high mistletoe low lantana ('mistletoe'), low mistletoe high lantana ('lantana'), high mistletoe high lantana ('mistletoe & lantana') and low mistletoe low lantana ('control'). The control and mistletoe and lantana matrices were built directly from the transitions of individuals in the plots under those conditions. As mistletoe only affects vital rates

(growth, survival, reproduction) of adults (Sinha & Bawa 2002; Setty Siddappa 2004), to build 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. To identify the effects of invasive species over time, separate matrices were created for each treatment starting from 1999, even though invasion only occurred later.

In *P. indofischeri*, invasion of mistletoe and lantana occurred much later than in the *P. emblica* plots. Mistletoe reached moderate levels in 2006 in four of the plots and remained at the low densities in the rest (Table 1). We built low and high mistletoe treatment matrices directly from the transitions of individuals in those conditions.

We built 40 matrices for *P. emblica* (one annual matrix for each of four treatments * 10 years) and 20 for *P. indofischeri* (one annual matrix for each of two treatments * 10 years) (Appendix S2, Supporting Information). For each matrix, we calculated the projected population growth rate, λ, (the rate at which a population would grow over the long-term under the parameterization conditions (Caswell 2001)) and determined the 95% per cent confidence intervals of λ with 2000 bootstrap runs (Caswell 2001).

CALCULATION OF STOCHASTIC AND TRANSIENT GROWTH RATES

We calculated stochastic population growth rates (λ_s) for both species under pre/low invasion (1999–2002) and high invasion (2006–2009) contexts (Stubben & Milligan 2007, Appendix S1, Supporting Information). Lantana cover began increasing in *P. indofischeri* plots in 2008 but was still fairly low and spread across all plots. We therefore simulated the effects of high lantana cover on *P. indofischeri* λ_s by building matrices using the transitions for seedlings and saplings from the *P. emblica* plots with high lantana.

There were no unharvested amla populations in BRT. However, NTFP harvest was banned in BRT in 2006. Therefore, we assessed the effects of fruit harvest with and without high levels of invasive species by simulating fruit harvest in the 2006–2009 matrices and calculating λ_s (Appendix S1, Supporting Information). We considered differences in λ and λ_s to be significant when confidence intervals did not overlap.

To assess the effects of invasive species and fruit harvest on indices of amla transient dynamics, we projected standardized

Table 1. Characteristics of amla populations used to build matrix models. All treatments had no (or very low) mistletoe or lantana when the experiments were established in 1999

		Mistletoe level*		Lantana cover†		Fruit harvest‡	
	Treatment	By 2002	2006–2009	By 2002	2006–2009	1999–2005	2006–2009
Phyllanthus emblica	Control	Low	Low	Low	Low	Yes	No
	Mistletoe	Moderate	High	Low	Low	Yes	No
	Lantana	Low	Low	Moderate	High	Yes	No
	Mistletoe & lantana	Moderate	High	Moderate	High	Yes	No
Phyllanthus indofischeri	Control	Low	Low	Low	Low	Yes	No
	Mistletoe	Low	Moderate	Low	Low	Yes	No

*% trees infected with mistletoe: low: < 5; moderate: 35–45; high: > 90.
†Lantana cover (%): low: < 5; moderate: 30–50; high: > 90.
‡After the harvest ban in 2006, the effects of fruit harvest were simulated using values from 1999 to 2005.

mean matrices from 2006 to 2009 for each treatment and species, with and without fruit harvest. We used the standardized observed population structure at our last census as the initial population structure (Stott, Townley & Hodgson 2011, Appendix S1, Supporting Information).

ELASTICITIES AND LIFE TABLE RESPONSE EXPERIMENTS

We calculated elasticity values of the matrix elements for each of our 60 matrices. Elasticity values were summed per stage-class (Appendix S1, Supporting Information). We carried out fixed, one-way life table response experiments (LTRE, Caswell 2001) among treatments and time periods within and between species, when $\Delta\lambda$ was large (>0·05). We used the mean matrix for each treatment or time period (Appendix S1, Supporting Information). All demographic analyses were carried out using the popbio (Stubben & Milligan 2007) and popdemo (Stott *et al.* 2012) packages in R 2.14 (R Development Core Team 2011).

Results

For *P. emblica*, between 55% and 65% of fruit produced was harvested in most years. No *P. indofischeri* trees were harvested in years when fruit production was low, but up to 88% of fruit was harvested when production was higher (Fig. 1). Harvesters only harvested from trees with high fruit crops. For harvested trees, 93·8 ± 0·08% and 94·3 ± 0·09% of fruit were removed for *P. emblica* and *P. indofischeri*, respectively. When fruit production was low in either species, harvest rates of both dropped. For example, the low rate of *P. emblica* harvest in 2003 was a result of low fruit production in *P. indofischeri* that year. Low population-level yields in either species reduce total economic returns as well as returns per time invested.

EFFECTS OF FRUIT HARVEST AND INVASIVE SPECIES ON DETERMINISTIC POPULATION GROWTH RATES

Before and during the early stage of mistletoe and lantana invasion, λ values for *P. emblica* and *P. indofischeri* were similar across treatments and tended to be <1 for *P. emblica* and ≥1 for *P. indofischeri* (Fig. 2). For *P. emblica*, λ for control plots increased after 2004 but remained significantly <1 in most years.

Once mistletoe reached moderate levels (Table 1), it decreased λ in both species, dropping to as low as 0·76 in some years for *P. emblica* mistletoe plots (Fig. 2). In contrast, lantana, with or without mistletoe, did not decrease *P. emblica* λ values. For this species, the lack of adult mortality observed in 2009 is likely an artefact of the small remaining adult sample size ($N = 13$).

EFFECTS OF FRUIT HARVEST AND INVASIVE SPECIES ON STOCHASTIC POPULATION GROWTH RATES

For both species, pre-invasion λ_s were similar across treatments; these were significantly <1 for *P. emblica* and signifi-

cantly >1 for *P. indofischeri* (Appendix S1 Fig. S1, Supporting Information). Mistletoe significantly decreased λ_s for both species and pushed *P. indofischeri* λ_s significantly <1(Fig. 3).

Lantana, with or without mistletoe, had no added effect on λ_s for *P. emblica*. For *P. indofischeri*, model simulations of lantana invasion significantly decreased λ_s compared to control plots, but the drop was less than that caused by mistletoe: 5·4 (5·3–5·6)% vs. 7·5 (7·4–7·6)%, respectively. Simulations of mistletoe & lantana invasion decreased λ_s by approximately the sum of their individual effects (a drop of *c.* 13% with respect to the control; Fig. 3b).

Simulations of fruit harvest after the ban (2006–2009) show that it had no effect on λ_s in *P. emblica* control plots nor in those invaded by mistletoe, lantana or both (Fig. 3a). For *P. indofischeri,* fruit harvest simulations decreased λ_s in control plots, but it remained significantly >1 and the decrease was significantly less than that caused by either mistletoe or lantana invasion (Fig. 3b). Fruit harvest decreased λ_s by a similar amount in control and mistletoe plots. However, fruit harvest had no effect on λ_s in lantana or in lantana & mistletoe plots (Fig. 3b).

(a) $N = 247$

(b) $N = 239$
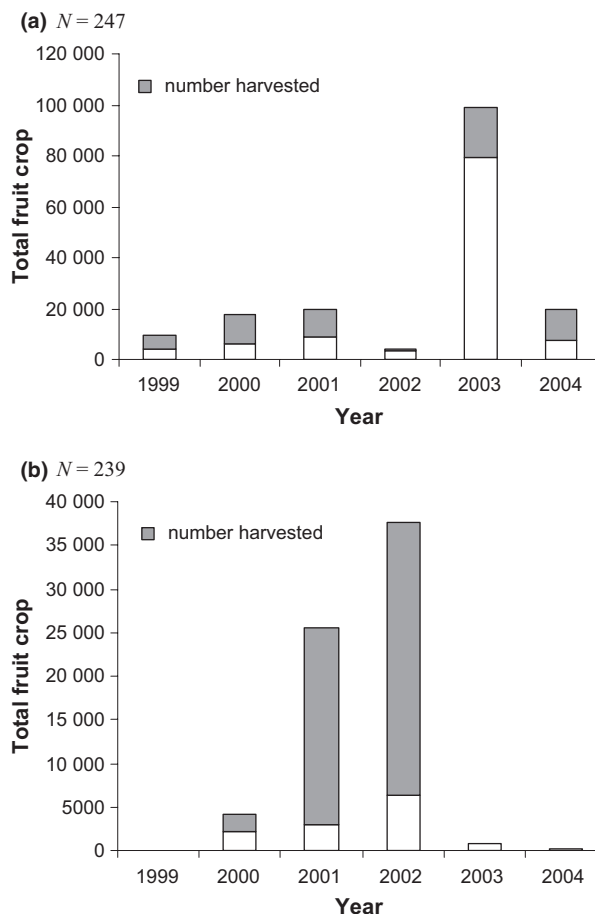
Fig. 1. Fruit crop and proportion of amla fruit harvested per year for (a) *Phyllanthus emblica* and (b) *Phyllanthus indofischeri* in BRT, before the harvest ban. Values include unharvested and harvested trees. At the individual level, a mean of 94% of fruit was removed per harvested tree for both species.
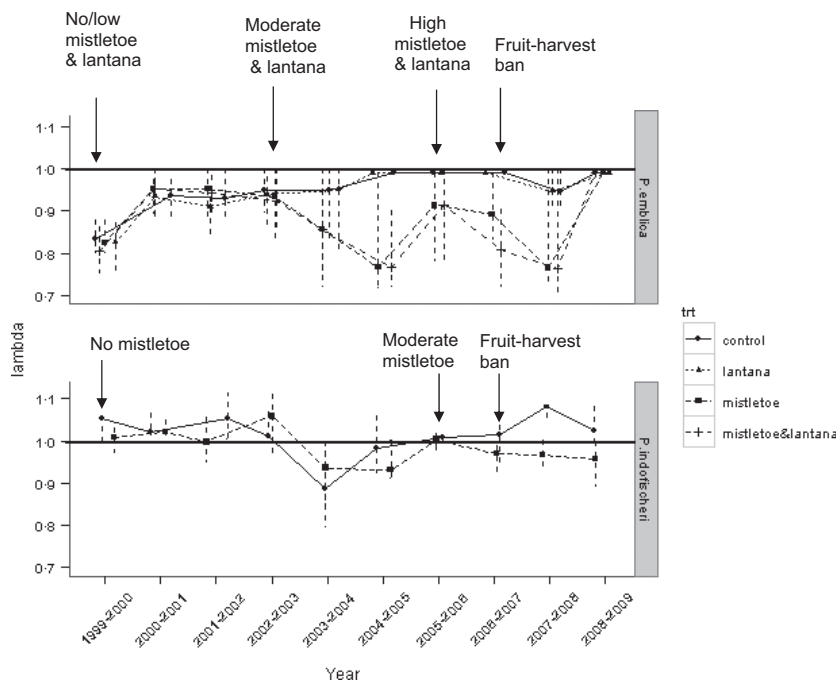
Fig. 2. Projected long-term population growth rates λ (jittered) for *Phyllanthus emblica* and *Phyllanthus indofischeri* populations subject to high vs. low/no levels of the invasive mistletoe *Taxillus tomentosus* and the invasive understory shrub *Lantana camara* from 1999 to 2009. Error bars represent 95% confidence intervals. λ < 1 indicates projected population decline.

(a) *Phyllanthus emblica*

(b) *Phyllanthus indofischeri*
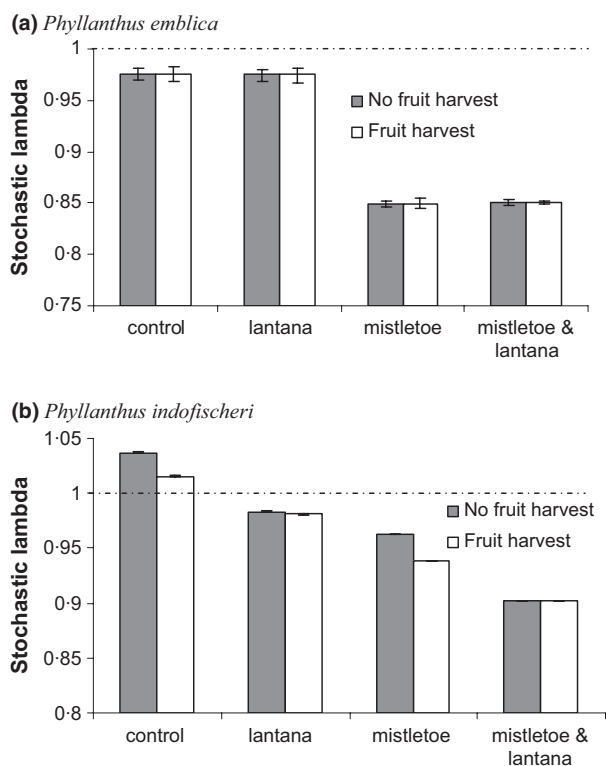
Fig. 3. Effect of invasive species (mistletoe *Taxillus tomentosus* and shrub *Lantana camara*) and fruit harvest on amla stochastic population growth rates (λ_s). λ_s were derived from annual matrices from 2006 to 2009, when invasive species levels were high. Error bars represent 95% confidence intervals. λ_s < 1 indicate projected population decline.

EFFECTS OF FRUIT HARVEST AND INVASIVE SPECIES ON TRANSIENT DYNAMICS

For both species, the combined effects of mistletoe and lantana resulted in short-term population decline at a faster rate than asymptotic decline (e.g. faster than that expected of a population starting with the same structure but with stable growth; see inertia values Appendix S1 Table S1, Supporting Information). For control, mistletoe and lantana plots, the reverse was true, because the densities of seedlings and saplings in these plots increased faster than in a population with stable growth. However, for control, mistletoe and mistletoe & lantana plots, the density of *P. indofischeri* reproductive-size individuals decreased at a faster rate than asymptotic decline (Table S1, Supporting Information).

In general, fruit harvest reduced densities of saplings relative to unharvested populations, but did not affect reproductive-size individuals (Table S1, Supporting Information). However, for *P. indofischeri* mistletoe plots, the difference between transient and asymptotic decline of adults was greater with fruit harvest than without. For both species, the density of reproductive-size individuals in plots with mistletoe is expected to decrease by 50% in about 8 years. For *P. emblica* control and lantana plots, this figure is 25% in < 15 years (Fig. 4).

EFFECTS OF FRUIT HARVEST AND INVASIVE SPECIES ON AMLA ELASTICITY

For *P. emblica*, the elasticity of survival was dominant in all years and treatments (mean over time ranged from 0·97 to 0·99

(a) *Phyllanthus emblica* (> 9 cm dbh)

(b) *Phyllanthus indofischeri* (>5 cm dbh)
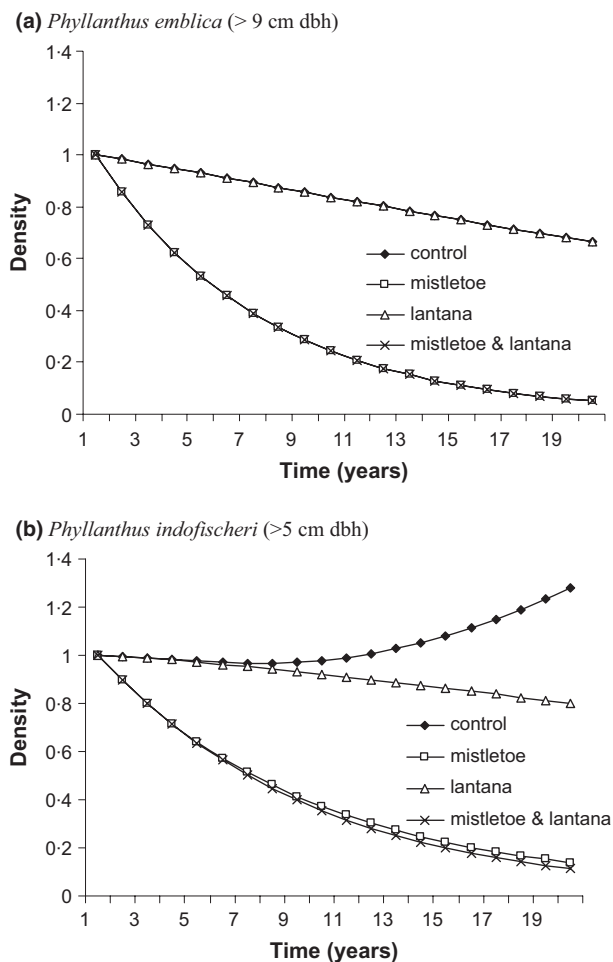
Fig. 4. Transient dynamics of amla individuals of reproductive size. Projections were based on the standardized, observed population structure at the last census and mean matrices from 2006 to 2009.

across treatments, Appendix S1 Fig. S2, Supporting Information). Elasticity of reproduction was always < 0·01. Differences in the elasticity values among stage-classes discussed below are essentially differences in the elasticity of survival.

For *P. emblica* control plots, in most years, but especially since 2003, the elasticity structure was dominated (> 0·99) by the large adults (Fig. 5a). The pattern was similar for plots invaded by lantana, except that large adults had higher values in the 1999–2003 period as lantana was increasing (Fig. 5b). Elasticity of *P. emblica* in plots invaded by mistletoe was also similar (Fig. 5c), but in 2006–2007, elasticity was dominated by small and medium saplings. The elasticity structure in mistletoe & lantana plots was slightly more dominated by small and large adults from 1999 to 2003 than in mistletoe plots and, after 2003, completely dominated by the large adults (Fig. 5d).

For *P. indofischeri,* elasticity of survival was dominant but lower than that of *P. emblica*, with values ranging from 0·78 to 1 in both treatments (mean = 0·89 and 0·91 for control and mistletoe plots, respectively, Appendix S1 Fig. S2, Supporting Information). Elasticity of reproduction was < 0·02 in all years and treatments.

In *P. indofischeri* control plots, small and large adults tended to have the highest elasticity values, but in some years large saplings also had high values (Fig. 5e). The invasion of mistletoe (after 2005) shifted the elasticity structure so that it was either dominated by large adults or by small or medium saplings (Fig. 5f).

LIFE TABLE RESPONSE EXPERIMENTS

For *P. emblica*, the single contributor to the higher λ observed in control vs. mistletoe plots was increased adult survival (Fig. 6a). In contrast, for *P. indofischeri*, higher rates of adult stasis, growth and reproduction and growth of medium saplings were all contributors to the higher observed λ in control vs. moderate mistletoe plots (Fig. 6b). For *P. emblica*, lower survival and growth of small and medium saplings were the contributors to the lower λ in mistletoe & lantana plots vs. mistletoe plots, in 2006–2007 (Fig. 6c).

In control plots, higher growth of medium saplings made a large contribution to the higher λ observed in *P. indofischeri* vs. *P. emblica* populations. Increased small sapling growth and adult survival also made contributions (Fig. 6d).

In *P. indofischeri*, a big contributor to the 2 years with λ < 1 was decreased survival of large adults, although smaller decreases in reproduction as well as in stasis and growth of the smaller stages also played a role (Fig. 6e–f).
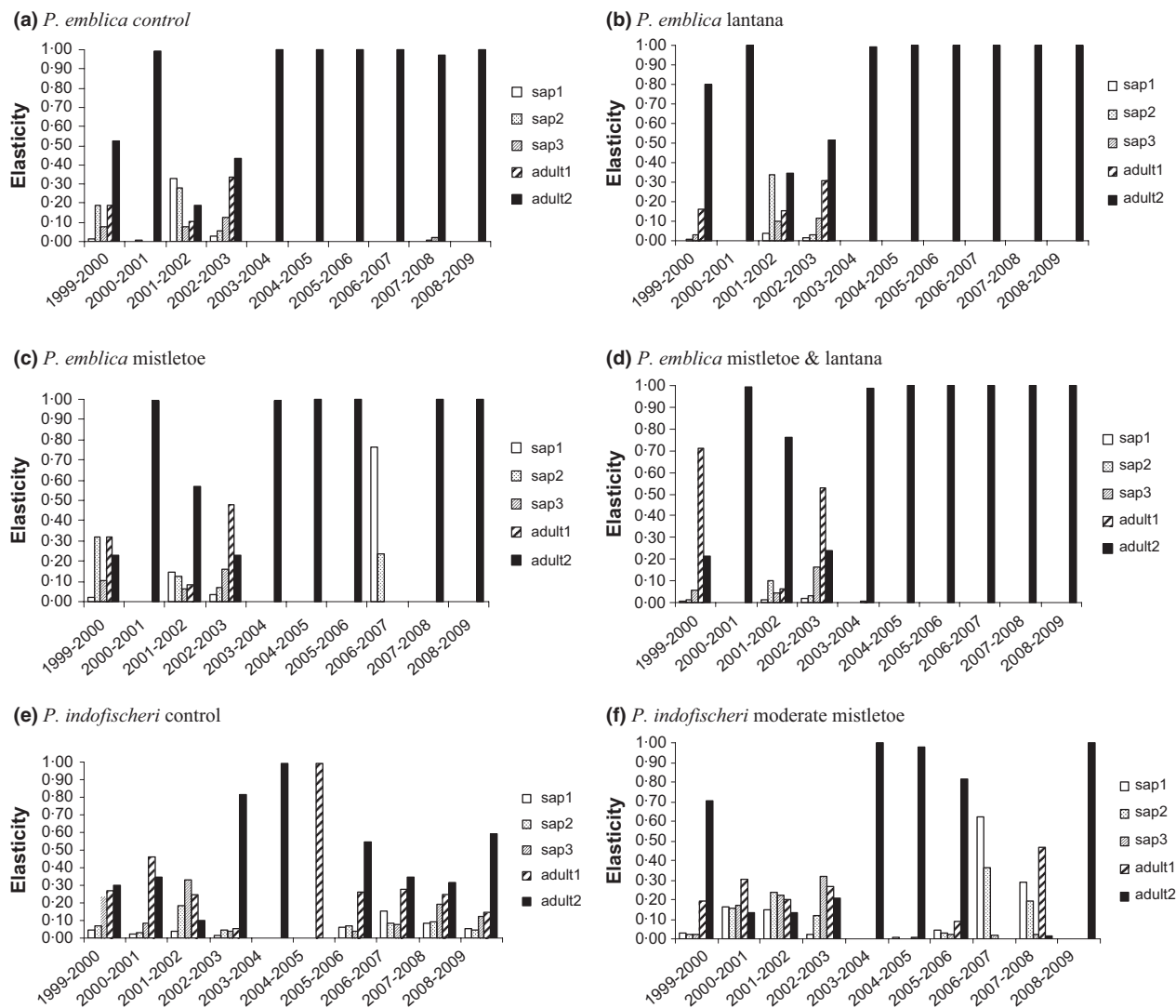
Discussion

EFFECTS OF FRUIT HARVEST

Heavy fruit harvest has been assumed to be the principle driver of amla decline but our results suggest that it appears to have little impact on amla population dynamics. This is apparent from the very low elasticity of fruit production as well as from the results of fruit harvest simulations on long-term and transient dynamics. In addition, for *P. indofischeri,* λs were significantly > 1 during fruit harvest years. Sexual reproduction in woody species tends to have low elasticity (Franco & Silvertown 2004), and some woody species can tolerate harvest of 80–90% of fruit (Ticktin 2004). As harvesters only harvest fruit from trees with very large crops, and only in years when reproduction is high, most amla trees are not harvested more than once every 2 or 3 years. This probably fosters at least periodic regeneration for many individuals. In plots without invasive species, both species showed good recruitment of seedlings, regardless of the level of fruit harvest. 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 species facing similar situations.

EFFECTS OF MISTLETOES

In contrast to fruit harvest, mistletoe invasion had a large negative effect on populations of both species because of increased adult mortality. When populations were invaded

(a) *P. emblica control*

(b) *P. emblica* lantana

(c) *P. emblica* mistletoe

(d) *P. emblica* mistletoe & lantana

(e) *P. indofischeri* control

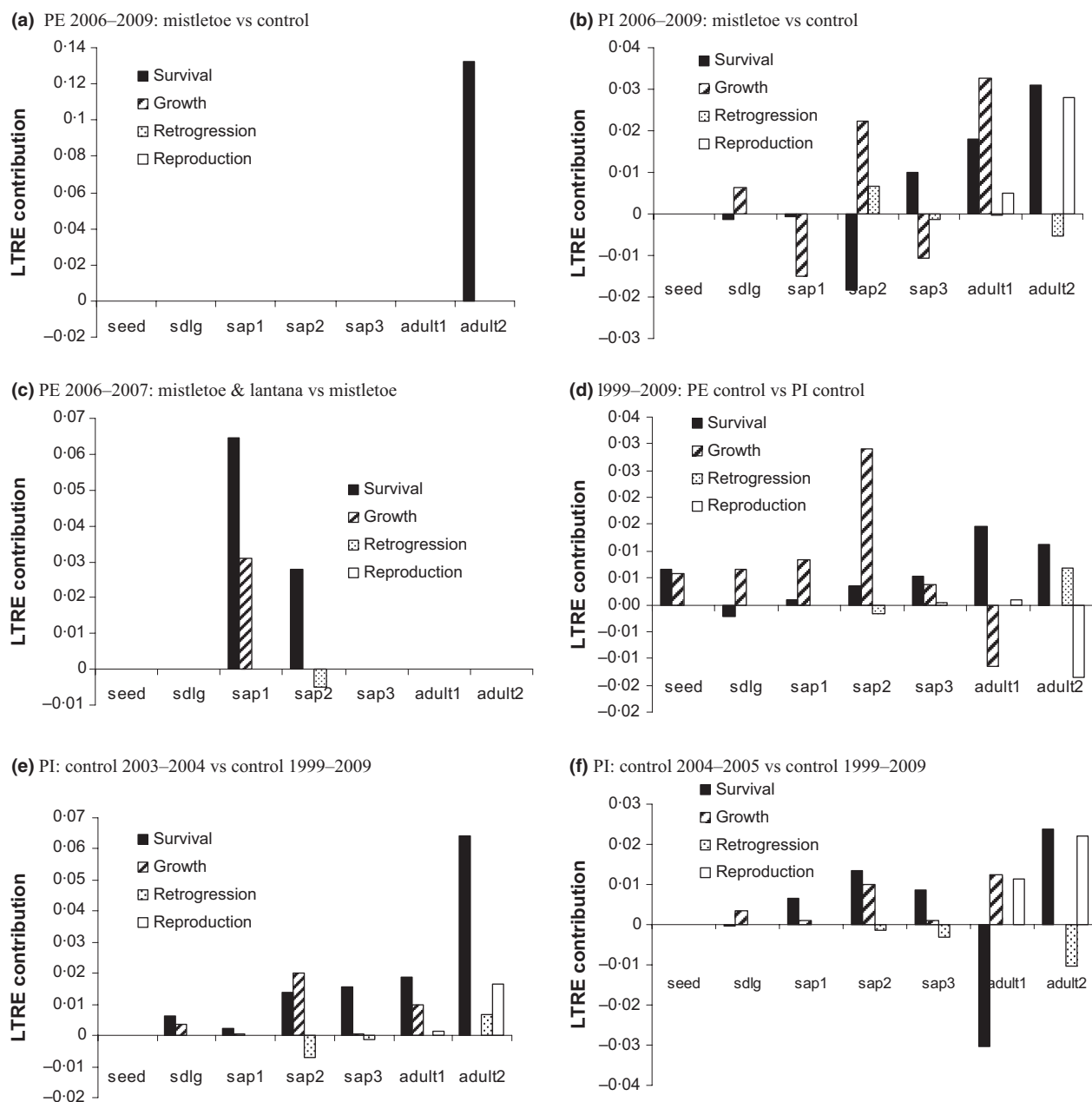**(f)** *P. indofischeri* moderate mistletoe

Fig. 5. Elasticity values per stage-class for amla populations subject to high vs. low/no levels of the invasive mistletoe *Taxillus tomentosus* and the invasive understorey shrub *Lantana camara* from 1999 to 2009. Seeds and seedlings have elasticities < 0·01 for all years and are not shown here.

by mistletoes, λ_s dropped significantly, consistent with the high elasticity values of adult survival in most years. Adult survival tends to have high elasticity in woody species (Franco & Silvertown 2004) and mistletoes can increase host tree mortality in other systems (Reid, Stafford Smith & Venables 1992; Spurrier & Smith 2007). However, this is the first study to identify their impacts on host long-term population growth.

The expansion of mistletoe in BRT and elsewhere is probably a consequence of changes in land management. Fire can regulate mistletoe populations elsewhere (Norton & Reid 1997; Fadini & Lima 2012), and the Soliga maintain that mistletoes have increased because their traditional use of fire was banned when BRT became a sanctuary. Like indigenous forest communities world-wide (Berkes 2008), the Soliga annually set low-intensity fires to increase the visibility of wild animals, keep forest weeds and tick populations in check, regenerate grass growth for their cattle and control mistletoe populations.

Our results illustrate that mistletoe control is both essential and urgent (Fig. 4). Unfortunately, low-intensity fires are no longer possible given the high flammability of lantana. The traditional practice of lopping branches may be the only viable management.

However, mistletoe invasion alone cannot explain the decline in *P. emblica* because populations had relatively high adult mortality and $\lambda_s < 1$ before mistletoe invaded the study plots. The causes of this mortality are unclear, but were consistent across plots and other parts of the BRT (Setty Siddappa 2004). There were no signs of a previous large-scale disturbance. One explanation is that, like other mistletoe host species, *P. emblica* trees naturally have a fairly rapid turnover. In Australia, *Acacia victoriae* trees host a *Loranthus* mistletoe, but in the absence of mistletoe, they also have very short life spans and annual mortality rates of about 10% (Reid & Stafford Smith 2000). This is similar to the observed annual *P. emblica* mortality over that period.

Fig. 6. Life Table Response Experiments for amla populations subject to high vs. low/no levels of the invasive mistletoe *Taxillus tomentosus* and the invasive understorey shrub *Lantana camara*. Analyses are based on mean matrices for the time periods indicated. Positive values represent contributions to higher long-term population growth rates (λ_s) observed in the treatment or time period listed second in each comparison. PE, *Phyllanthus emblica*; PI, *Phyllanthus indofischeri*.

However, while *A. victoriae* adult mortality is balanced by equal recruitment, *P. emblica* had high seedling recruitment but almost no recruitment from small saplings into larger stage-classes (> 1 cm d.b.h.). The current elasticity structure of *P. emblica*, dominated entirely by survival of reproductive adults, is a consequence of the bottleneck in the regeneration pathway. In contrast, between 5% and 20% of *P. indofischeri* small saplings grew to 1 cm d.b.h. annually. The higher rates of growth and survival of *P. indofischeri* small and medium saplings were among the biggest contributors to the higher λ observed in *P. indofischeri* control plots.

DIRECT AND INDIRECT EFFECTS OF LANTANA

Direct and indirect effects of lantana are probably responsible for the surprisingly low growth of *P. emblica* saplings across all treatments, and therefore for the low λ_s before mistletoes invaded the study plots. Lantana cover was > 90% in lantana plots but this did not decrease λ_s compared to plots without lantana. Instead, growth of the small stage-classes in both control and lantana plots decreased markedly after 2002 and stayed low, and resprouting with multiple stems (seen as retrogression in the matrices) increased greatly over time, especially

in control plots. These patterns indicate increased grazing pressure in control plots and this result is corroborated by observations by the Soliga. Over our study period, the density of lantana increased over 10-fold in BRT's scrub and dry deciduous forests, and the total area covered by lantana doubled (Sundaram 2011). The Soliga maintain that the spread of a monotypic lantana understorey has greatly decreased the grazing area available to wild ungulates, subjecting the few remaining lantana-free areas to more intensive grazing. This is consistent with a lantana removal study in a nearby-protected area, which found no increase in tree seedling survival or growth after lantana removal and hypothesized that lantana is reducing the food supply for herbivores (Prasad 2010).

Grazing by ungulates causes significant decreases in long-term population growth rates in plant species (Maron & Crone 2006). While other factors such as fire and drought could also decrease growth and increase retrogression, these effects would be periodic (during and after the event) and not consistent over the 6-year period we observed.

These results illustrate the need to control lantana, but also highlight that lantana removal alone will not suffice as a strategy to increase population growth rates of NTFP species. Effective management regimes need to include a combination of lantana removal, granting permission to the Soliga to harvest lantana for firewood and 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.

COMBINED EFFECTS OF DISTURBANCES

Given the indirect effects of lantana on our control plots, the combined effects of lantana and mistletoe on *P. emblica* are difficult to distinguish from our data. However, when survival of small and medium saplings was higher than usual (2006–2007), at a level that might be typical without lantana or heavy grazing, the elasticity structure of populations in mistletoe plots shifted to seedlings and saplings, and the added effect of lantana then further decreased λ. This suggests that in areas where lantana is not widespread, and therefore increased grazing pressure in lantana-free areas has not yet occurred, the presence of lantana could further decrease populations that are already negatively affected by mistletoe. Our simulations of lantana invasion in *P. indoficheri* populations are consistent with this observation and indicate that the effects of lantana and mistletoe on *P. indofischeri* asymptotic dynamics are additive. In addition, although asymptotic dynamics in *P. emblica* mistletoe and mistletoe & lantana plots did not differ, transient analyses show that populations in mistletoe & lantana plots are expected to decrease more quickly over the short term than populations in mistletoe plots. This suggests that amla populations subject to both mistletoe and lantana are at greatest risk and should be targeted first.

In contrast to our expectations, the effect of fruit harvest on long-term amla dynamics does not appear to be exacerbated in the context of invasive species. For *P. indofischeri*, the combined effects of mistletoe and fruit harvest appear to be additive, while those of lantana and fruit harvest are subadditive. These results are consistent with those for *P. emblica*, where lantana had direct and indirect effects on all populations and fruit harvest had no added effect. This suggests that in the context of reduced regeneration of seedlings and saplings, a decrease in reproductive output owing to fruit harvest has little effect on long-term dynamics (even though it further reduces sapling densities in the short term). While there is still little information on interactions among drivers of population dynamics, under stressful conditions, the effects of additional disturbance may be lower than expected (Gaoue & Ticktin 2010). Nonetheless, for *P. indofischeri* in mistletoe plots, the difference between short term and asymptotic decline for both saplings and adults was greater when fruit harvest occurred.

The effects of NTFP harvest and invasive species on amla populations are probably complicated by variation in other natural and anthropogenic factors. A drought from 2002 to 2004 (Javeed *et al.* 2009) is probably the major contributor to the low λ in *P. indofischeri* during this period. Our LTREs showed that lower survival and growth across most stage-classes were the major contributors to the decrease in λ. The effects of drought may have been exacerbated in 2004–2005, when non-Soliga villagers from outside the BRT cut down small trees for firewood. 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.

The direct and indirect effects of invasive species have devastated BRT's *P. emblica* populations. In the mistletoe & lantana plots, the density of individuals < 1 cm d.b.h. decreased to < 10% of 1999 levels and the overall population to 16%. The total population in control plots was only 35% of the original in 1999. The declines in *P. indofischeri* are less pronounced and more recent, but this species appears to be heading in the same direction. Moreover, short-term declines in reproductive-size adults of this species are expected to be much faster than predicted by asymptotic dynamics. Lantana and mistletoe populations are widespread across Indian dry forests, inside and outside of protected areas, and this situation is probably common elsewhere. The endemic status of *Phyllanthus indofischeri* makes this species particularly vulnerable, and our results suggest that drought or consistent firewood harvest could cause further population decline.

IMPLICATIONS FOR POLICY AND FUTURE RESEARCH

Plant populations in the tropics are routinely subject to multiple sources of anthropogenic disturbance, but the magnitude of the individual and combined effects has rarely been examined. Our results illustrate that disentangling the effects of common disturbances is critical for developing effective management strategies. In the case of amla, we illustrated that the disturbance widely blamed for population decline (NTFP harvest) is not the lead cause of decline. Given that lantana affects amla both directly and indirectly – populations without any lantana also have low recruitment into the sapling stage –

it is easy to see how fruit harvest was misidentified as the driver of decline. Our relatively long-term data set allowed us to identify the indirect effects of lantana. This emphasizes the need for longer-term demographic studies to inform management practices.

Our results have important management and policy implications for NTFPs and other species. First, it should not automatically be assumed that harvest is the main cause of decline for NTFPs. The ban on NTFP harvest in protected areas is clearly not an effective conservation policy for amla, nor is this likely to be a successful management strategy for other NTFP species in similar situations. A recent review of NTFP harvest studies suggested that the effects of harvest on dynamics of many NTFP species may be confounded with other drivers, but that these have not been taken into consideration (Schmidt *et al.* 2011). Effective management requires addressing the drivers contributing most to population decline. Ineffective conservation policy for NTFP not only fails to conserve the target species, but also has negative consequences for the livelihoods of harvesters (e.g. Sandemose 2009).

Second, our results suggest that the main drivers of amla decline, mistletoe and lantana, are probably driving the decline of other Indian dry forest tree species. Amla is a preferred host of mistletoe, but it colonizes at least 14 other species (Rist *et al.* 2008, 2010). The regeneration bottleneck we found for *P. emblica* in lantana-free areas may be shared by the many other Indian dry forest tree species palatable to ungulate herbivores. While other studies have illustrated that tree regeneration can be suppressed under lantana stands (e.g. Gooden *et al.* 2009; Sundaram 2011), to our knowledge, this is the first study to indicate that lantana can indirectly limit recruitment in lantana-free areas through increased grazing by wild herbivores. These indirect effects could also be present in other lantana-invaded systems with large ungulate herbivore populations. If so, effective management will require targeting areas not yet invaded by lantana with measures such as small temporary exclosures.

This study illustrates the importance of disentangling the effects of different sources of anthropogenic disturbance on the demography of plant species of conservation concern. This approach is critical in other parts of Asia and Africa, where NTFP and other at-risk species are subject to multiple disturbances, and effective conservation policy and management requires identification of the most important drivers of decline.

Acknowledgements

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Supporting Information

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

Appendix S1. Calculation of demographic rates and model parameterization.

Appendix S2. Matrices for *Phyllanthus emblica* and *P. indofischeri*.

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