



Effects of Harvesting Flowers from Shrubs on the Persistence and Abundance of Wild Shrub Populations at Multiple Spatial Extents

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Abstract: *Wildflower harvesting is an economically important activity of which the ecological effects are poorly understood. We assessed how harvesting of flowers affects shrub persistence and abundance at multiple spatial extents. To this end, we built a process-based model to examine the mean persistence and abundance of wild shrubs whose flowers are subject to harvest (serotinous Proteaceae in the South African Cape Floristic Region). First, we conducted a general sensitivity analysis of how harvesting affects persistence and abundance at nested spatial extents. For most spatial extents and combinations of demographic parameters, persistence and abundance of flowering shrubs decreased abruptly once harvesting rate exceeded a certain threshold. At larger extents, metapopulations supported higher harvesting rates before their persistence and abundance decreased, but persistence and abundance also decreased more abruptly due to harvesting than at smaller extents. This threshold rate of harvest varied with species' dispersal ability, maximum reproductive rate, adult mortality, probability of extirpation or local extinction, strength of Allee effects, and carrying capacity. Moreover, spatial extent interacted with Allee effects and probability of extirpation because both these demographic properties affected the response of local populations to harvesting more strongly than they affected the response of metapopulations. Subsequently, we simulated the effects of harvesting on three Cape Floristic Region Proteaceae species and found that these species reacted differently to harvesting, but their persistence and abundance decreased at low rates of harvest. Our estimates of harvesting rates at maximum sustainable yield differed from those of previous investigations, perhaps because researchers used different estimates of demographic parameters, models of population dynamics, and spatial extent than we did. Good demographic knowledge and careful identification of the spatial extent of interest increases confidence in assessments and monitoring of the effects of harvesting. Our general sensitivity analysis improved understanding of harvesting effects on metapopulation dynamics and allowed qualitative assessment of the probability of extirpation of poorly studied species.*

Keywords: Allee effects, metapopulation dynamics, process-based models, serotinous Proteaceae, South African Cape Floristic Region, spatial scales, threshold behavior

Efectos de la Cosecha de Flores de Arbustos sobre la Persistencia y Abundancia de Poblaciones de Arbustos Silvestres en Escalas Espaciales Múltiples

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Resumen: *La cosecha de flores silvestres es una actividad económica importante de la cual se conoce poco de sus efectos ecológicos. Evaluamos el efecto de la cosecha de flores sobre la persistencia y abundancia de arbustos en escalas espaciales múltiples. Para este fin, construimos un modelo basado en procesos para examinar la persistencia y abundancia media de arbustos silvestres cuyas flores son sujetas a cosecha (Proteaceae serotinoso en la Región Florística Cabo de Sudáfrica). Primero, realizamos un análisis de sensibilidad general del efecto de la cosecha sobre la persistencia y abundancia en extensiones espaciales anidadas. La persistencia y abundancia de arbustos decreció abruptamente una vez que la tasa de cosecha excedió cierto umbral en la mayoría de las extensiones espaciales y combinaciones de parámetros demográficos. En extensiones mayores, las metapoblaciones soportaron tasas de cosecha altas antes de que su persistencia y abundancia decrecieran, pero la persistencia y abundancia también decrecieron más abruptamente debido a la cosecha que en las extensiones más pequeñas. Este umbral en la tasa de cosecha varió con la habilidad de dispersión de las especies, la tasa reproductiva máxima, la probabilidad de extirpación o extinción local, la intensidad de los efectos Allee y la capacidad de carga. Más aun, la extensión espacial interactuó con los efectos Allee y la probabilidad de extirpación debido a que ambos atributos demográficos tuvieron mayor efecto sobre la respuesta de poblaciones locales que sobre la respuesta de metapoblaciones. Subsecuentemente, simulamos los efectos de la cosecha sobre 3 especies de Proteaceae de la Región Florística del Cabo y encontramos que estas especies reaccionaron de manera diferente a la cosecha, pero su persistencia y abundancia decreció a tasas de cosecha menores. Nuestras estimaciones de las tasas de cosecha en la producción máxima sostenible fueron diferentes a las de investigaciones previas, quizá debido a que los investigadores utilizaron estimaciones de parámetros demográficos, modelos de dinámica poblacional y extensiones espaciales diferentes a las usadas por nosotros. Un buen conocimiento demográfico y la identificación cuidadosa de la extensión espacial de interés incrementan la confianza en evaluaciones y monitoreo de los efectos de la cosecha. Nuestro análisis de sensibilidad general mejoró el entendimiento de los efectos de la cosecha sobre la dinámica metapoblacional y permitió una evaluación cualitativa de la probabilidad de extirpación de especies poco estudiadas.*

Palabras Clave: comportamiento umbral, dinámica metapoblacional, efectos Allee, escalas espaciales, modelos basados en procesos, Proteaceae serotinoso, Región Florística Cabo de Sudáfrica

Introduction

The potential resolution of conflicts between commercial harvest and conservation of a species requires information about the effects of harvesting on that species (Mace & Reynolds 2001). In the South African Cape Floristic Region (CFR) and the Southwest Australian Floristic Region, where there are high concentrations of species richness and endemism, harvesting of flowers from wild plants is an economically important activity for which the ecological effects are poorly understood (e.g., Cowling & Lamont 1985; Lamont et al. 2001; Turpie et al. 2003). In the Cape Floristic Region, flower harvesting has substantial economic value (US\$13 million gross income in 1999), with the majority of this value resulting from the harvesting of Proteaceae inflorescences (Greyling & Davis 1989; Turpie et al. 2003), and relies mostly on wild populations (Turpie et al. 2003). About 100 species of CFR Proteaceae are economically important, more than 50 of which are serotinous shrubs that store their seeds in cones (Rebello 2001). But, it is unclear what level of harvest of flowers and cones the shrubs can tolerate without negative effects on the population (Maze & Bond 1996; Turpie et al. 2003).

A harvest-induced decrease in reserves of seed can affect population dynamics (e.g., adult abundance) if recruitment is limited by seed availability. Because most seeds of Proteaceae are dispersed over short distances, recruitment is limited by the number of seeds available, and this limitation generally increases as spatial extent

increases (Nathan & Muller-Landau 2000). Harvesting decreases the number of seeds available for dispersal and recruitment and thus may have pronounced effects on species abundance and persistence at large spatial extents. Additionally, seed availability may be even more limiting if Allee effects (a decrease in per capita reproduction at low densities) occur (Allee et al. 1949; Courchamp et al. 1999). Allee effects seem to shape the local and large-scale dynamics of certain Fynbos Proteaceae (Cabral & Schurr 2010) that have metapopulation dynamics (Schurr et al. 2007). Moreover, Allee effects can reduce population viability and alter a species' sensitivity to harvesting (Stephens & Sutherland 1999; Petersen & Levitan 2001). Nevertheless, even if harvesting reduces recruitment and promotes extirpation of local populations, persistence of the species over large extents will not necessarily be compromised for two reasons. First, metapopulation persistence may be unaffected by increases in probability of local extinction if colonization rates are sufficiently high (Levins 1969). Second, immigration from neighboring populations can counteract reduced reproduction via rescue effects (Brown & Kodric Brown 1977).

The effect of harvesting flowers of wild plants on plant dynamics may thus vary with species' demographic properties and with the spatial extent of the monitored metapopulation. The only study of the effects of flower harvesting on CFR Proteaceae (Maze & Bond 1996) was restricted to small spatial extents and did not use population models. Models describing how local

population dynamics are affected by long-distance dispersal have been developed recently and explain abundances over the entire range of CFR Proteaceae on the basis of species-specific demographic properties (Cabral & Schurr 2010). We used such a model to describe the demographic consequences of harvesting flowers from shrubs and applied it to different spatial extents to investigate whether populations of Proteaceae that extend over relatively larger areas are less negatively affected by increasing harvesting rates.

In contrast to most previous studies of the effects of harvesting on metapopulations (e.g., Tuck & Possingham 1994; Supriatna & Possingham 1998; Bascompte et al. 2002), we used spatially explicit process-based models to simulate metapopulation responses to harvesting over large geographical areas with explicit local population dynamics. To improve general understanding of harvesting effects on metapopulations, we conducted a sensitivity analysis in which we varied demographic properties and the spatial extent at which harvesting was assessed. Subsequently, we simulated harvesting effects on two species of Proteaceae that occur in the CFR.

Methods

Study System

The population dynamics of serotinous CFR Proteaceae are driven by recurrent fire, which triggers dispersal and recruitment (Bond & van Wilgen 1996). Because recruitment and recruit mortality occur only immediately after a fire, the population dynamics of Proteaceae proceed in discrete time steps determined by fire-return intervals (Bond et al. 1995), which on average vary spatially from 10 to 30 years (van Wilgen 1987; Polakow & Dunne 1999; Wilson et al. 2010). Serotinous Proteaceae that produce sprouts can survive fire as adults and are iteroparous with overlapping generations, whereas species that do not sprout persist after fire through seeds and are semelparous with nonoverlapping generations (Bond & van Wilgen 1996; Bond & Midgley 2001, 2003). Competition reduces seed set of individual plants, but does not cause substantial adult mortality (Bond et al. 1995). Similarly, Allee effects in Proteaceae affect individual fecundity, but not adult survival (Lamont et al. 1993), and seem to shape dynamics of certain species across large areas (Cabral & Schurr 2010). If the fire-return interval is short (e.g., 2–8 years), populations of species that do not sprout and are not sexually mature can be extirpated (Bond & van Wilgen 1996). Fires associated with such extirpations are typically small due to low levels of flammable biomass and are less likely to occur than the cyclical large fires. Harvesting of flower heads does not increase the number of seeds in remaining flower heads (Mustart & Cowling 1992).

Process-Based Model

We used C++ to implement our demographic models of CFR Proteaceae (Cabral & Schurr 2010). For a given spatial grid (cell size 1' × 1' [longitude vs. latitude]; approximately 1.55 × 1.85 km for the Cape Floristic Region), our demographic models described the persistence and abundance of local populations connected through long-distance seed dispersal. The demographic processes of density-dependent seed production, seed dispersal, recruitment, adult mortality, and local extinction or extirpation were simulated once per time step. We modeled these processes with parameters that represented maximum per capita rate of reproduction, carrying capacity, per-fire adult mortality, per-fire local extinction probability, Allee critical point (minimal viable size of local populations in the absence of immigration), and a discrete two-dimensional dispersal kernel that yielded the probability of seed dispersal from a source cell to neighboring cells (Table 1). Parameter values in the model were constant over all suitable grid cells and for different ages of individuals of species that sprout. Recruitment and mortality during periods between fires were not included in the model. Because fire was not simulated explicitly, variation in fire size, intensity, and season were also not included. Extirpation associated with fire randomly affected individual grid cells independent of other cells. Alternative model versions differed in the density-dependence of local population growth (Cabral & Schurr 2010).

Each model simulation had as input a grid of patches that were either suitable or unsuitable for local populations. All suitable cells were initialized with populations at carrying capacity. How suitability and carrying capacity were described in the model varied depending on whether the model was applied for sensitivity analyses or for selected CFR Proteaceae species and is, thus, specified separately below. After model simulations reached the quasi-stationary state, we simulated harvesting of flowers from wild shrubs by removing a portion (harvest rate, H) of the seeds produced in a cell within a time step. Effects of harvesting may be overestimated if one assumes harvest rate is constant rather than spatially and temporally heterogeneous.

Sensitivity Analyses

We conducted full-factorial sensitivity analyses by varying species' characteristics within realistic ranges of values (Table 1). To describe species with different long-distance dispersal ability, we used discrete versions (5 × 5 grid cells) of a generalized exponential kernel (Clark et al. 1998). The kernels had mean dispersal distance of 0.1 cells and shape parameters of 1 and 0.5 that yielded thin-tailed negative exponential and fat-tailed dispersal kernels, respectively. To describe local population

Table 1. Model types and demographic properties used in the full-factorial sensitivity analysis and to simulate harvesting impacts on three species of Proteaceae.

Model and parameters	Sensitivity analyses	Proteaceae species		
		Protea compacta	Protea neriifolia	Protea repens
Local population model	Beverton-Holt + Allee effects	Beverton-Holt	Ricker + Allee effects	Ricker + Allee effects
Demographic parameters				
probability of local extinction (E)	0.001, 0.01, 0.1, 0.25	0.1	0.002	0.0001
mortality rate (M)	0.05, 0.25, 0.50, 0.75, 1	1	1	1
maximum reproductive rate (R_{\max})	1.5, 5.5, 12.5, 18.5	1.5	15.1	2
carrying capacity (K , ind/ha)	174, 1744, 5000, 10000	87	14764	38.27
Allee critical point (C , ind/ha) ^a	$-K$ (absent), $-K/2$ (weak), $0.05K$ (strong)	-	-0.003	0.08
Dispersal model	spatially explicit model for generalized exponential kernel (Clark et al. 1998); mean distance, 0.1; cell lengths; shape parameter, $c = 1$ (thin-tailed kernel) or $c = 0.5$ (fat-tailed kernel)	mechanistic model for primary air-borne (Tackenberg 2003) and mechanistic model for the secondary tumble (Schurr et al. 2005) seed dispersal by wind, both validated for each species (Schurr et al. 2007)		

^aAbundance at which the population is affected by Allee effects.

dynamics, we used the Beverton–Holt model (Beverton & Holt 1957) with Allee effects (see Cabral & Schurr 2010). Harvest rate varied from 0% to 100% in steps of 4%.

For each combination of species' characteristics (or parameter values) and H , we ran the model on 100 fractal landscapes of 129×129 cells; 5% of the cells were suitable for local populations. This means the landscapes had unsuitable and suitable cells and that suitable cells were arranged in a fractal fashion. We chose sizes of fractal landscapes and proportions of suitable cells because they could be computed quickly and would be comparable to the extent and patchiness of the habitat of many CFR Proteaceae species. We used the midpoint displacement algorithm with fractal dimension of 2.2 and variance in displacement of 30 (Saupe 1988) to aggregate fractal distributions of habitat. We investigated the effect of spatial extent of habitat by calculating the proportion of persisting metapopulations in nested regions. These regions represented local (1 cell) and three regional (small regional, 9×9 cells; regional, 33×33 cells; large regional, 129×129 cells) extents. For each landscape, we first selected a suitable cell at random as the local extent. To obtain regional extents the model symmetrically expanded extent from the focal cell (Fig. 1). Each simulation initially ran for 300 time steps, which was sufficient for reaching the quasi-stationary state. Subsequently, harvesting took place throughout the grid for 500 time steps to allow detection of harvesting effects even for species that, if harvested, need long periods to reach the quasi-stationary state.

Persistence, Abundance, and Harvesting Thresholds

We investigated persistence and overall abundance on the basis of the ecology of Proteaceae. We calculated per-

sistence for each parameter combination, spatial extent, and harvest rate as the proportion of the 100 simulation replicates that survived to the end of the simulation (500 time steps). For subsequent analyses, we determined the harvest rates at which persistence and overall abundance

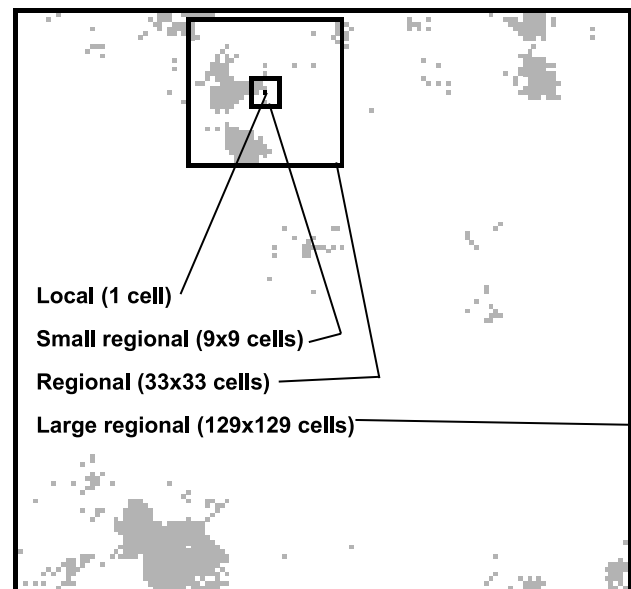


Figure 1. Spatial extents (local, small regional, regional, and large regional) used to study effects of harvesting flowers from wild shrubs (Proteaceae), at nested spatial extents in a sensitivity analysis. Entire grid is 129×129 cells, and habitat is in grey. For each one of the 100 landscapes a focal cell that contains habitat is randomly selected and used as the central cell of 9×9 and 33×33 grid-cell subregions (rectangular frames).

decreased to $\leq 90\%$ of their values without harvest (P_{90} and A_{90} , respectively). Although these criteria are arbitrary, a 10% decrease in abundance or persistence is used by the International Union for Conservation of Nature (IUCN) to characterize species in the Red List category vulnerable (IUCN 2001). Rates of harvest at which persistence and abundance fell to 50% and 10% of their without-harvest values were qualitatively similar to P_{90} and A_{90} (results not shown). We also calculated harvest rates associated with occupied range, but they were highly correlated with P_{90} (Spearman's rank correlation 0.945), so we did not include it in our analyses. For some parameter combinations (low local extinction probability and adult mortality), individual plants persisted in all simulation replicates, even at a 100% rate of harvest. In these extreme cases, we assumed $P_{90} = 100\%$.

Statistical Analyses

We summarized the outcomes of the sensitivity analyses by fitting linear models with harvest rates that had an effect as the response variable. We transformed to the arcsine the harvest rates that had an effect to ensure normality of errors. The maximum linear model (i.e., the model with the greatest number of terms) for each analysis included all two-way interactions between extent of habitat and species' parameters. To obtain minimal adequate models, we removed terms from the maximum model as long as this caused no significant decrease in model fit at $p < 0.05$ (Crawley 2005).

Model Application to Selected CFR Proteaceae

We assessed how harvesting of flowers would affect persistence and abundance of three species of Proteaceae (*Protea compacta*, *P. neriifolia*, and *P. repens*). Cabral and Schurr (2010) developed an approach that allows model selection and estimation of the demographic parameters from abundance records for CFR Proteaceae (Rebello 2001, 2008). To estimate parameters that describe local abundance and persistence, we used species-specific dispersal kernels derived from validated mechanistic models for seed dispersal by wind (Tackenberg 2003; Schurr et al. 2005, 2007). By statistically comparing alternative models of local population dynamics, Cabral and Schurr (2010) found that the model with local population dynamics following the Beverton-Holt function (Beverton & Holt 1957) best described the range of *P. compacta*. For this species, we used parameter estimates from Cabral and Schurr (2010). By applying Cabral and Schurr's (2010) approach, we found that abundance distributions of *P. neriifolia* and *P. repens* over large extents were best described if the Ricker model with Allee effects fitted local population dynamics (Supporting Information).

Table 1 summarizes the population models and parameter estimates for study species. Although *P. neriifolia* and *P. repens* have similar vegetative forms and would be expected to have carrying capacity (K) around 4000–8000 individuals/ha, our estimated K was an average in which inhabitable and uninhabitable (e.g., rock outcrops or water bodies) portions of bioclimatically suitable cells were integrated. We described areas that are bioclimatically suitable for each study species with species-specific distribution models estimated from species occurrences and climatic variables observed in the CFR (Midgley et al. 2003). We ran 50 replicate simulations per harvest rate (from 0% to 100% in steps of 1%). Before the onset of harvesting, simulations ran for 1000 time steps to ensure the metapopulation dynamics were quasi-stationary.

For the study species, we calculated A_{90} , P_{90} , and the harvest rate at maximum sustainable yield. Thus, we could compare our results for *P. neriifolia* and *P. repens* with existing estimates of maximum sustainable yield (Maze & Bond 1996). Yield was the number of seeds (as a surrogate for flower heads) harvested across the species' global range. At the last time step, we averaged yields over all replicates. Thereafter, we identified the harvest rate that maximized average yield. Furthermore, for each species we quantified how uncertainty in parameter estimates affected assessments of the effects of harvesting. To this end, we determined multivariate 95% confidence intervals for model parameters with likelihood-ratio tests (Bolker 2008). For harvest simulations with parameters sets that varied within these confidence intervals, we estimated 95% confidence intervals for P_{90} , A_{90} , and harvesting rate at maximum sustainable yield.

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Results

Sensitivity Analyses

In general, harvesting decreased persistence probability and abundance. At most spatial extents and for most combinations of demographic parameters, persistence and abundance decreased abruptly once harvest rate exceeded a certain value, which can be considered a threshold (Fig. 2). This threshold was most abrupt at the largest extents, whereas at smaller extents increases in harvesting were associated with more gradual decreases in persistence and abundance (Fig. 2). When levels of persistence and abundance decreased sharply as harvesting increased relative to levels without harvesting, P_{90} coincided with or was close to the points of abrupt change in trend (Fig. 2). Exceptions to this trend occurred at small extents when there was a high probability of local extinction; the decrease in persistence was more gradual. Abundance of each species was more sensitive to harvesting than persistence: the harvest rate associated with a 10% reduction in abundance (A_{90}) was consistently lower than the corresponding harvest rate associated with a 10% reduction in

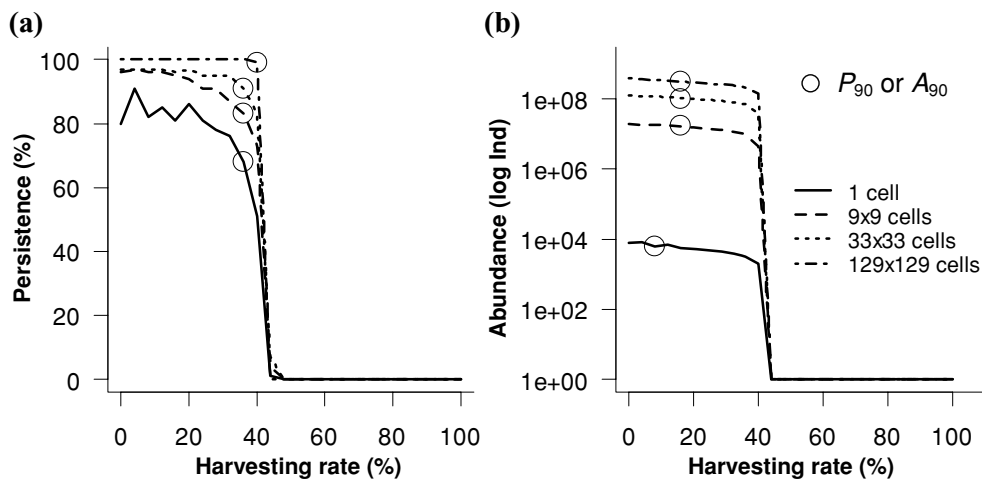


Figure 2. Effects of harvesting flowers from wild shrubs on (a) persistence and (b) abundance of metapopulations of Proteaceae species at different spatial extents (grid cell always has same size; metapopulations differ in size). Results shown are for one combination of demographic parameters that makes the difference between extents more evident ($E = 0.1$, $R_{max} = 5.5$, $K = 1744$ individuals/ba, $C = 0.05K$, $M = 1$, fat-tailed dispersal kernel (higher long-distance dispersal ability, obtained for the generalized exponential kernel with mean distance equal to 0.1 cell lengths and shape parameter $c = 0.5$, see Clark et al. 1998), where E is probability of local extinction, R_{max} is maximum reproductive rate, K is carrying capacity, C is Allee critical point; and M is mortality rate). The y-axis in (b) is plotted on a log scale. Harvest rates that have an effect, P_{90} and A_{90} , are the harvest rates at which the metapopulation persistence and overall abundance, respectively, are $\leq 90\%$ of the values without harvesting.

persistence (P_{90} , Fig. 3). Nevertheless, both persistence and abundance responded similarly to variation in demographic parameters and spatial extent (Fig. 3). The effect of harvesting (as indicated by low P_{90} and A_{90} harvesting rates) was strongest at the local extent (Figs. 3a-b) and for species with thin-tailed dispersal kernels, low maximum reproductive rates, strong Allee effects (Figs. 3c-d), and high probability of extirpation (Figs. 3e-f).

In addition to the main effects of demographic parameters and spatial extent on abundance and persistence, effects of harvesting also depended on the interaction of some demographic parameters with spatial extent, as revealed by the two-way interactions retained in minimally adequate models for P_{90} and A_{90} (Fig. 4). In the absence of Allee effects, persistence was reduced more by harvesting at the local extent than at all other extents (lower P_{90} at the local spatial extent), whereas when Allee effects were weak or strong the effect of harvesting was similar across all extents (Fig. 4a). Moreover, when probability of extirpation was high, the effect of harvesting was also greater at local extents than at all larger extents, whereas no such extent dependence of harvesting effects occurred when probability of extirpation was not high (Fig. 4b). Plant abundances depended only on the two-way interaction between spatial extent and probability of extirpation and were consistently lowest at the local extent (Fig. 4c). Although the strongest differences in species response to harvesting occurred between the local extent and the other extents (Fig. 4), excluding the

local extent did not qualitatively change outcomes of our statistical analyses (results not shown).

Specific CFR Proteaceae

The three study species differed quantitatively in their projected response to harvesting of their flower heads. Persistence and abundance of *P. compacta* and *P. nerifolia* were projected to be affected range wide by very low harvest rates, whereas *P. repens* was projected to be affected above moderate harvest rates (Figs. 5a-b). The persistence of all species was projected to be unaffected by harvesting up to a threshold level of harvest that coincided with the P_{90} harvest rate that had an effect (Fig. 5a). The abundance of *P. compacta* and *P. nerifolia* was also projected to be unaffected by harvesting up to a threshold level of harvest. By contrast, the effect of harvesting on abundance of *P. repens* was more complex; abundance initially decreased as harvest rate increased (reaching A_{90} at 5% harvesting), but with intermediate harvest rates abundance increased and then decreased quickly to extinction (Fig. 5b).

Abundance of the three study species was more sensitive to harvesting than persistence: A_{90} estimates were lower than the P_{90} estimates. The A_{90} estimates were 1% (95% CI 1–1%), 2% (2–6%), and 5% (2–21%) for *P. nerifolia*, *P. compacta*, and *P. repens*, respectively. The P_{90} estimates were 6% (6–8%), 15% (15–64%), and 48% (7–48%) for *P. nerifolia*, *P. compacta*, and *P. repens*,

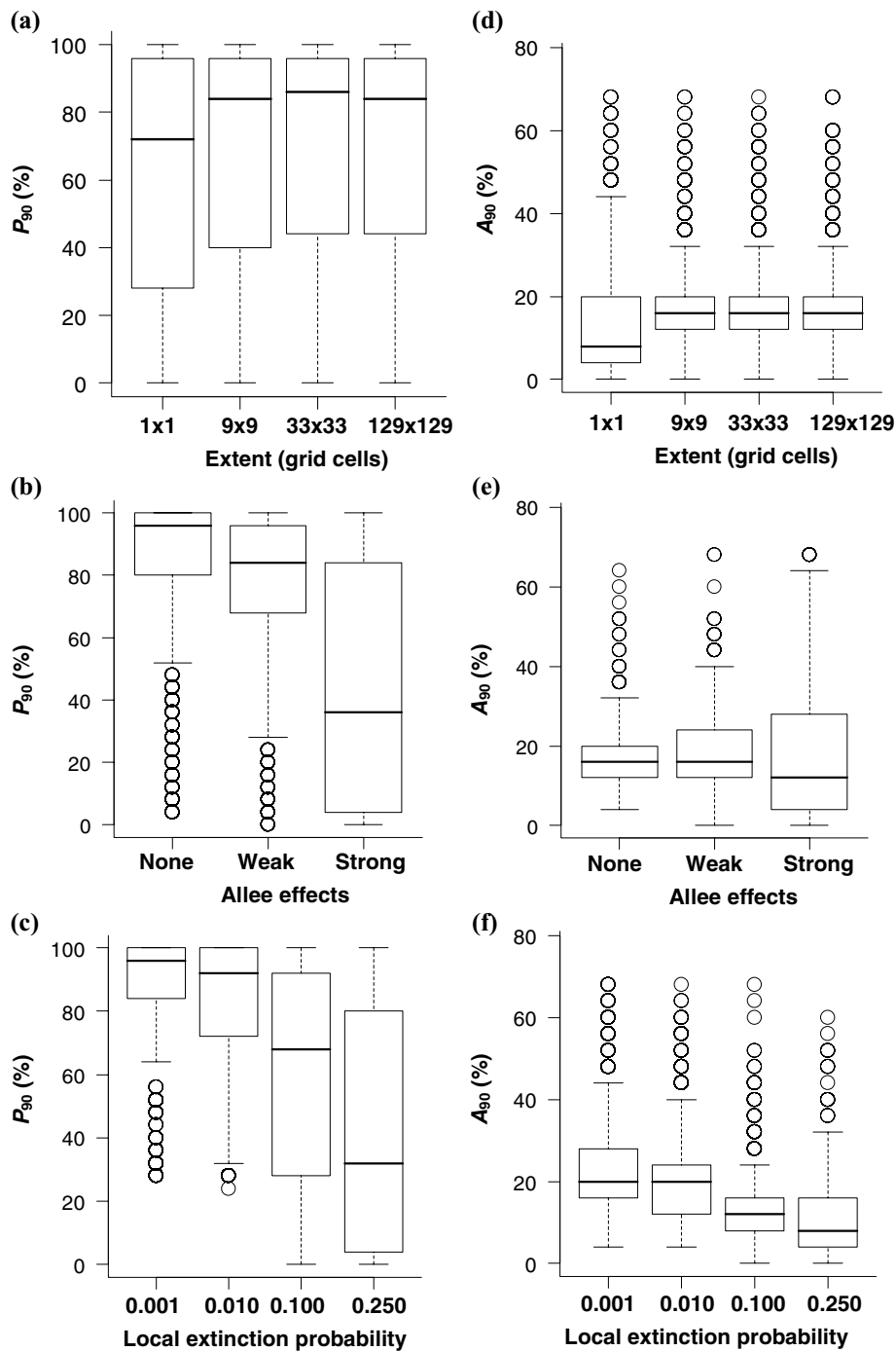


Figure 3. Effects of spatial extent of the metapopulation, Allee effects, and local extinction probability (parameters that varied in the sensitivity analyses) on the harvest rates of flowers from wild shrubs (Proteaceae species) at which persistence and abundance are $\leq 90\%$ of the level without harvesting (P_{90} [a, b, c], A_{90} [d, e, f], respectively). Whiskers represent 1.5 interquartile range, whereas circles are outliers.

respectively. The effect of the harvest rates associated with 10% reductions in persistence and abundance on the projected range of *P. compacta* at the last simulated time step diverged (Figs. 6c-d). The harvest rate that had an effect on persistence (P_{90}) of this species markedly decreased range size, whereas the abundance-based harvest rate that reduced abundance by 10% (A_{90}) had a negligible effect on occupied range (Figs. 6c-d). The harvest rates at maximum sustainable yield were 4% (95% CI:

4–6%), 7% (7–34%), and 45% (3–45%) for *P. neriifolia*, *P. compacta*, and *P. repens*, respectively.

Discussion

The effect of flower harvesting on persistence and abundance of Proteaceae on the basis of the taxon’s ecology varied as a function of species’ demographic parameters

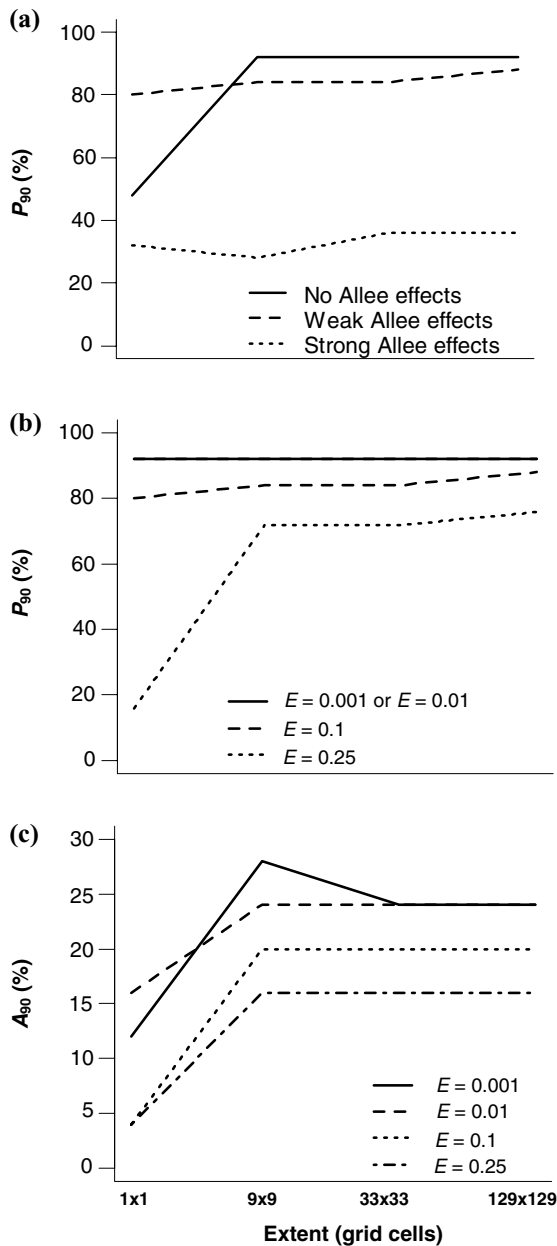


Figure 4. Effects of interactions between spatial extent of metapopulation and (a) Allee effects and (b, c) probability of local extinction (E) of Proteaceae on the harvest rates that have an effect, P_{90} and A_{90} (harvest rates of flowers from wild shrubs at which persistence and abundance, respectively, are $\leq 90\%$ of the level without harvesting). Results are for one combination of demographic parameters: $R_{max} = 5.5$, $K = 1744$ individuals/ha, $M = 1$, fat-tailed dispersal kernel (higher long-distance dispersal ability, obtained for the generalized exponential kernel with mean distance equal to 0.1 cell lengths and shape parameter $c = 0.5$, see Clark et al. 1998), where R_{max} is maximum reproductive rate, K is carrying capacity, and M is mortality rate.

and spatial extent (Figs. 2–4). Despite this variation, however, harvest of flowers from shrubs generally reached a threshold level after which persistence and abundance decreased sharply (Figs. 2 & 5).

Harvesting Effects on Proteaceae

Two of three study species (*P. compacta* and *P. nerifolia*) were very sensitive to harvesting; very low levels of harvest affected the species' persistence and abundance (P_{90} and A_{90} , Fig. 5). The fact that abundance and occupied range were more sensitive to harvesting than persistence (Figs. 3 & 5) indicates that species abundance (e.g., A_{90}) is a better measure of the effects of harvest than species persistence (e.g., P_{90}). The abundance of species may decrease rapidly if their flowers are harvested at rates that reduce persistence by 10% (P_{90}) (P_{90} generally coincided with or was close to harvest thresholds) (Figs. 2 & 5). Hence, if persistence is an objective, monitoring the effect of harvest rate on abundance (e.g., A_{90}) should be more effective in informing actions aimed at species persistence than monitoring the effect of harvest rate on persistence (e.g., P_{90}). In reality we would expect harvest rates to be lower than the rate of harvest that affected persistence or abundance because we did not model environmental stochasticity, which may cause an abrupt decline in abundance of populations (Lande et al. 2001).

The model results for abundance of *P. repens* seem related to differences in local abundance of the species. Such differences may originate from the model of local dynamics we selected for this species (Ricker model with Allee effects), which causes large fluctuations in abundance of local populations. The dynamics of populations for which abundance fluctuates substantially can be stabilized by harvesting some or all of the seeds that surpass the number needed to maintain a nonoscillatory population (Sinha & Parthasarathy 1996). Hence, for species with local populations that oscillate substantially in abundance, such as *P. compacta*, harvesting may stabilize abundance and probability of persistence of the species. Nonetheless, abundances were always highest without harvesting (Fig. 5b). For *P. repens* and *P. compacta*, model uncertainty (Jeltsch et al. 2008) seemed small because for both species a single model explained the empirical data markedly better than alternative models (Supporting Information). Nonetheless, for both species parameter uncertainty (Jeltsch et al. 2008) resulted in relatively broad confidence intervals at all harvest rates. But, our best estimate of harvest rate at maximum sustainable yield for *P. repens* (45%) matched independent empirical findings well ($\sim 50\%$ harvest rate; Maze & Bond 1996).

In contrast, our very low estimate of harvest rate for the maximum sustainable yield of *P. nerifolia* (4%) deviated from the estimate of Maze and Bond (1996) ($\sim 75\%$). This discrepancy is unlikely to have arisen from

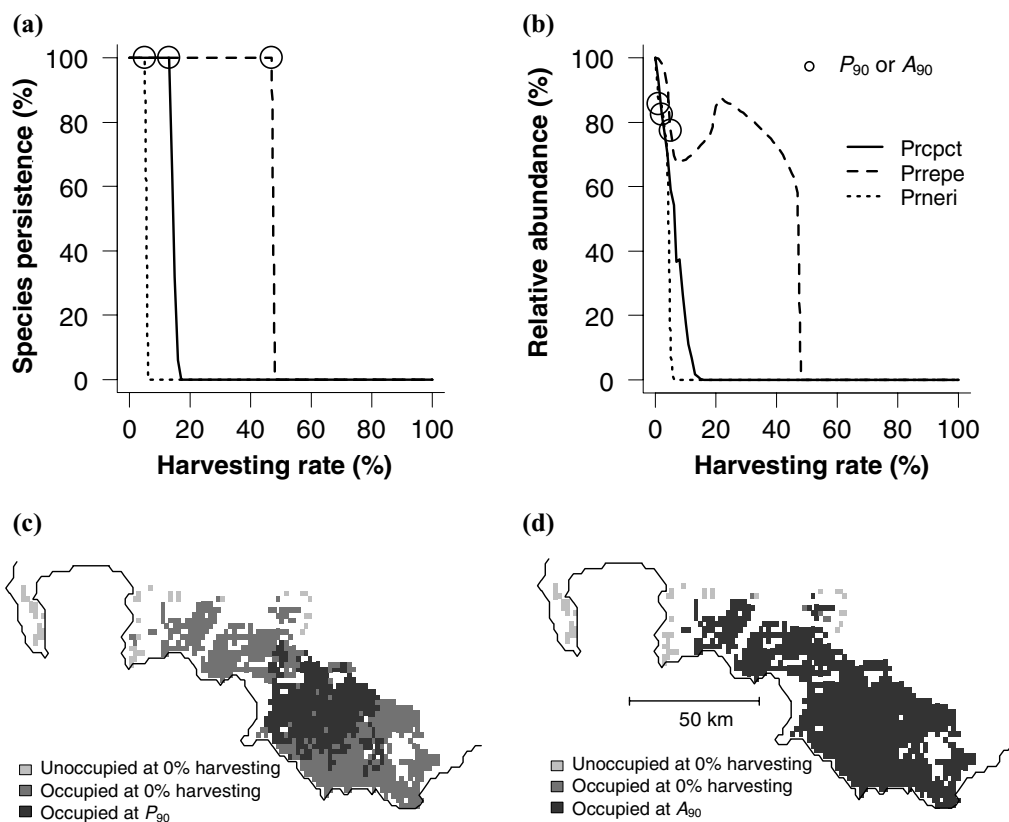


Figure 5. Effects of flower harvesting on three species of Cape Floristic Region Proteaceae in the last simulated time step of the model: (a) species persistence relative to harvest rate and (b) relative effect of harvest on abundance (*Prcpct*, *P. compacta*; *Prneri*, *P. neriifolia*; *Prrepe*, *P. repens*; circles, P_{90} in [a] or A_{90} in [b]). Examples of the effects of flower harvesting on the range of *P. compacta* at harvest rates that have an effect, (c) P_{90} or (d) A_{90} (defined in Fig. 2 legend) (black, cells occupied by the species at the harvest rates that have an effect; dark grey, cells occupied at 0% harvest; light grey, unoccupied potential habitat at 0% harvesting).

model or parameter uncertainty (Jeltsch et al. 2008) because the model selected for *P. neriifolia* was clearly better than other models we considered (Supporting Information), and maximum sustainable harvest rate had a narrow 95% CI. Therefore, the discrepancy in estimates of maximum sustainable yield may originate from diverging demographic parameters. Our estimates were averages over large spatial extents in which suitable and unsuitable portions of grid cells were integrated and our environmental parameters differed from Maze and Bond's (1996). The spatial extent (10×10 m) of their empirical study was much smaller than the local extent (one grid cell: 1.55×1.85 km) we used in our model.

Additionally, the difference between the estimated harvest rate associated with maximum sustainable yield of *P. neriifolia* may be associated with the model we selected for *P. neriifolia* (Ricker with Allee effects) and the estimated high reproductive rate. The Ricker model with Allee effects causes oscillatory and even chaotic local population dynamics when reproductive rates are high. Low model and parameter uncertainty indicated the species has complex population dynamics (also sug-

gested empirically by Bond et al. 1995). Maze and Bond (1996) did not account for such complex dynamics.

Harvesting Effects on Metapopulations

We expected persistence and abundance of metapopulations to be reduced more substantially by harvesting when colonization at larger extents was limited by seed availability (Nathan & Muller-Landau 2000). Apparent rescue effects and recolonization, however, buffered the extent to which abundance and persistence were limited by seed availability following harvest. These buffering effects are indicated by the fact that as spatial extent of metapopulations increased, persistence and abundance of metapopulations were less affected by harvesting (Fig. 2). Beyond a threshold harvesting rate, however, rescue effects and recolonization did not compensate for the reduction in abundance and persistence caused by harvesting and the metapopulations collapsed (Fig. 2).

Threshold harvesting rates were well approximated by the impacting harvest rate at which persistence was

reduced to 90% of the persistence without harvesting (P_{90} in Fig. 2). Threshold harvesting rates varied as a function of demographic properties (Figs. 3 & 5), but were relatively constant across spatial extents (Figs. 2 & 3). Nevertheless, the opposing effects of harvesting and rescue effects and recolonization caused metapopulations with larger extents to decrease more sharply after the harvest threshold was reached than metapopulations with small extents (Fig. 2). Such declines have been observed (Ludwig et al. 1993; Myers et al. 1995; Jackson et al. 2001). Harvesting may cause metapopulations to decline to a number of populations and to a total abundance below which extinction is inevitable (Hanski et al. 1996; Bascompte et al. 2002). Even if harvesting does not cause extinction, however, species or metapopulation recovery after harvesting ceases may be slow (Musick 1999), especially under Allee effects (Myers et al. 1995; Petersen & Levitan 2001), and may lead to a lower number of populations at which metapopulations are stable (Hanski et al. 1995). In practice for Proteaceae, it might be difficult to observe metapopulation collapses because harvesting of flowers is spatially heterogeneous.

Spatially explicit models allow the assessment of harvesting effects at multiple spatial extents. This multiextent assessment may be particularly valuable for species with a high probability of extirpation that do not have Allee effects because for these species harvest rates associated with decreases in abundance and persistence differ largely between local and larger extents (Fig. 4). This difference in the level of harvest that has an effect at local and larger extents is consistent with the finding that minimum population size, which is an abundance below which the population cannot persist (an abundance threshold at local spatial extent), does not correlate with the probability of extinction at large extents (Brook et al. 2006). This means accurate estimation of probabilities of both species extinction and population extirpation may require monitoring or assessments at multiple extents. Brook et al. (2006) found the divergence between the minimum population size and the probability of large-scale extinction without considering Allee effects. In species without Allee effects, assessments of harvesting at local extents may lead to lower estimated harvest rates associated with reductions in abundance and persistence because local populations are more affected by harvesting than metapopulations. Nevertheless, basing estimates of harvest rates that have an effect on data from large-scale assessments may lead to the extirpation of local populations. Hence, we believe assessments of harvesting effects should identify the spatial extents at which harvesting effects should be evaluated. Nevertheless, at smaller extents (e.g., flower farms), population extirpation thresholds are reached more gradually than at larger extents (Fig. 2). This gradual move toward the threshold may be due to the fact that increased harvest

has immediate effects at local extents, whereas at larger extents it is buffered by rescue effects.

In addition to probability of local extinction, maximum reproductive rate, adult mortality, and Allee effects, dispersal ability also influenced the effects of harvesting on species' persistence (Fig. 3) because as distances increased, availability of seeds of species with thin-tailed dispersal kernels decreased to a greater extent than that of species with fat-tailed kernels (Nathan & Muller-Landau 2000). These effects of dispersal ability on response to harvesting are characteristic of metapopulations, whose persistence depends on dispersal among patches (e.g., Levins 1969; Lindenmayer & Possingham 1996; Casagrandi & Gatto 2002).

Potential Applications to other Species

Our approach can serve to assess potential harvesting impacts on other CFR Proteaceae, for which sustainable yields and harvest rates associated with decreases in abundance and persistence have not been evaluated (Turpie et al. 2003). It has been projected that CFR Proteaceae will undergo large range shifts as climate changes (Bomhard et al. 2005; Midgley et al. 2006; Keith et al. 2008), and harvesting may decrease the ability of Proteaceae, especially dispersal-limited species that sprout (Higgins et al. 2008), to migrate. Process-based models, like ours, can address effects of climate change because they directly simulate range dynamics (Travis 2003; Keith et al. 2008; Cabral & Schurr 2010). Furthermore, our framework is transferable to other species and systems. Species-specific knowledge of key demographic processes can be applied within the framework to determine impacting harvest rates. Even if biological knowledge of a species or group of species is incomplete, our general sensitivity analysis can help to qualitatively assess possible responses of species to different levels of harvest.

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Supporting Information

Methods and results of model selection for the studied Proteaceae (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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